THE SPATIAL ORGANIZATION AND HABITAT SELECTION PATTERNS OF BARREN-GROUND GRIZZLY BEARS IN THE CENTRAL ARCTIC

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ABSTRACT

I studied the population delineation, hierarchical habitat selection, home range requirements, and denning habits of barren-ground grizzly bears (*Ursus arctos*) in Canada's central Arctic. To meet study goals, I tracked 81 grizzly bears equipped with satellite radio-collars in a study area of approximately 235,000 km^2, centred 400 km northeast of the city of Yellowknife, Northwest Territories. I identified three populations of grizzly bears in the study area using multivariate cluster analysis of movement data and population range analyses. High exchange among population units for both females and males, however, suggests that identified grizzly bear population units cannot be managed independently from one another. Using resource selection functions, I examined habitat selection patterns of grizzly bears first at the level of the home range (second order selection), and then within home ranges (third order selection). Second order selection analysis compared the proportional availability of habitats in the home ranges of grizzly bears to the proportional availability of habitats in the study area. At the third order of selection, habitat use determined from individual satellite telemetry locations was compared to the availability of habitats within home ranges of individual animals. For both levels of analysis, habitat availability was determined from classifed Landsat Thematic Mapper (TM) scenes covering a 75,000 km^2 representative portion of the study area. The general pattern at the second order of selection was for bears to possess home ranges, relative to the study area, that contained preferential amounts of esker habitat, tussock/hummock successional tundra, lichen veneer, birch seep, and tall shrub

riparian areas over other habitats. At the third order of selection, esker and riparian tall shrub habitats were the most preferred habitats by bears throughout the year. I also observed a general pattern of avoidance by females with cubs for habitats that were highly ranked by males. Annual ranges of males ($\overline{X}$ = 7,245 km^2) were significantly larger than the annual ranges of females ($\overline{X}$ = 2,100 km^2). Ranges presented in this study are the largest ranges yet reported for grizzly bears in North America. Multiple regression revealed that ranges increased in size as the proportional amount of poor bear habitat in the environment increased, supplying a constant amount of quality habitat to grizzly bears. Compared to the proportional availability of habitat types in the study area, esker habitat was selected for denning more than expected by chance. The majority of bears emerged from their dens in the last week of April (males) and first week of May (females). Den entrance occurred primarily in the last two weeks of October (females prior to males).

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How fortunate I am.

P. D. M.

30 August, 2000

DEDICATION

This thesis is dedicated to my wife, Michelle, and to my parents, Jim and Anne.

P. D. M.

30 August, 2000

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1. GENERAL INTRODUCTION

1.1 Background and Rationale

Although most grizzly bear (*Ursus arctos*) populations in North America have undergone some decline or range reduction subsequent the arrival of Europeans, populations of barren-ground grizzly bears inhabiting Arctic regions of North America have remained relatively undisturbed by European settlement. Far removed from human habitation, barren-ground grizzly bears have not been subjected to the exploitation and habitat changes that led to the extirpation of grizzly bears from much of their former range. Nonetheless, all populations of grizzly bears in Canada—including barren-ground populations—are classified as "vulnerable" and considered susceptible to population decline, largely because the species' is slow to reproduce (late age at maturity, small litter sizes, long interbirth intervals) and is relatively rare (Committee on the Status Of Endangered Wildlife in Canada, 1991, List of species at risk, Canadian Wildlife Service, Ottawa, Ontario, Canada).

Barren-ground grizzly bears in Canada's central Arctic (Fig. 1.1), however, may be at particular risk to population decline for several reasons: (1) they have limited continuity with other grizzly bear populations because they are near the northern and easternmost limit of the species' North American range, (2) because of reduced cover, bears in tundra habitats are more likely to be displaced by nearby

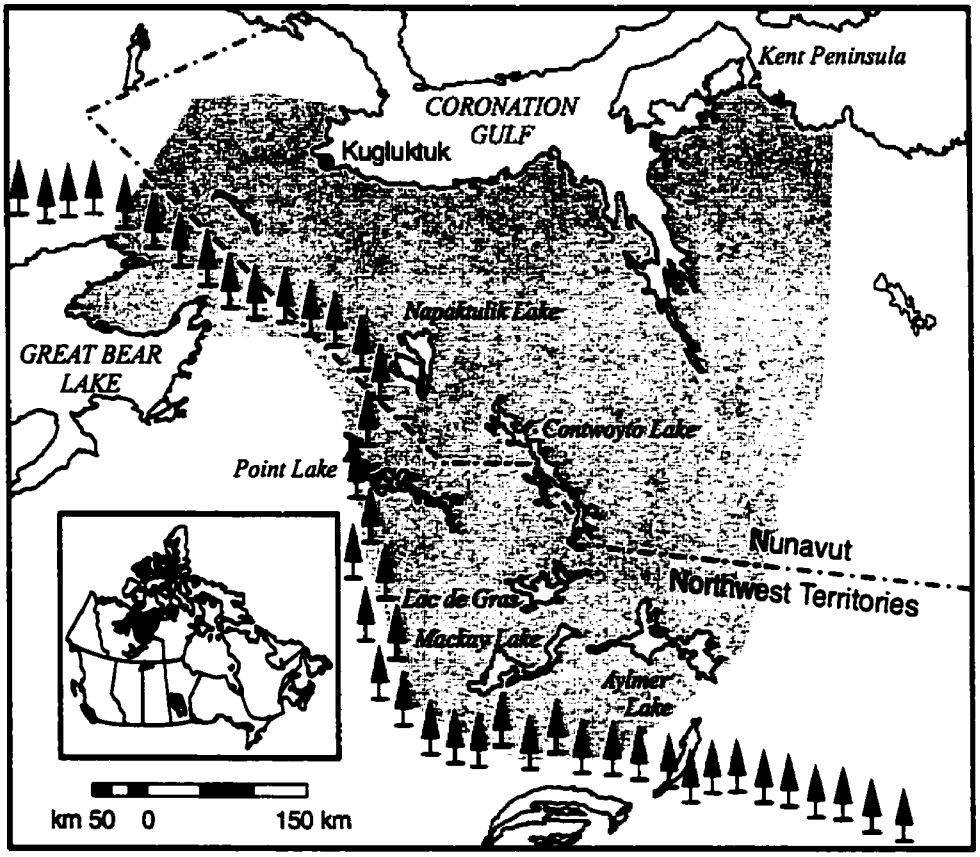

Fig. 1.1. Bounds of the study area used in this thesis (shaded region) in Canada's central Arctic. The treeline indicates the northernmost extent of coniferous forest in the study area.

human activity than bears in forested areas (McLellan 1990), (3) populations of grizzly bears in tundra habitat exist at the lowest recorded densities of all extant North American grizzly bears (review in McLellan 1994), and (4) they likely have very large spatial requirements (see, e.g., Reynolds 1980; Nagy et al. 1983; Clarkson and Liepins 1989; Ballard et al. 1993), which would put individual bears in contact with humans even when developments are at considerable distance from the core of the home range of an animal.

Adding to concerns over barren-ground grizzly bear conservation in Canada's central Arctic, recent discoveries of diamonds, gold, and base metals in the region have been targeted for large-scale mining operations. The Governments of Nunavut and the Northwest Territories support exploration and mining as long as such activities do not unduly impact the environment or its wildlife populations. Agencies such as the Federal Department of Indian Affairs and Northern Development, First Nations groups, the World Wildlife Fund, and the Canadian Arctic Resources Committee have all recognized the need for a conservation strategy to protect barren-ground grizzly bears in the area. In addition, mining companies (e.g., BHP Diamonds Inc., Diavik Diamonds Mines Inc.) have committed themselves to the concept of "sustainable development", thus supporting steps to mitigate the negative effects of resource exploration and extraction on barren-ground grizzly bears. Although it is agreed that grizzly bears in the central Arctic must be protected, knowledge of the ecology of bears in the region is limited and currently impairs the development of management strategies that would achieve this goal (Government of the Northwest Territories, 1991, Discussion paper towards the development of a Northwest

Territories barren-ground grizzly bear management plan, Yellowknife, Northwest Territories, Canada). There is a need to acquire ecological information on barren-ground grizzly bears to ensure that resource development does not result in substantial impacts on the population. Specifically, better understanding of the spatial organization, general habitat requirements, home range requirements, and denning requirements of grizzly bears in the central Arctic is needed before an effective management plan for the species can be developed.

1.2 Objectives

1.2.1 Population Delineation of Barren-Ground Grizzly Bears in the Central Arctic

In light of the need for ecological information on barren-ground grizzly bears and the need to develop a scientifically-based management plan for bears in the central Arctic, the first objective of this research project was to identify possible sub-populations of grizzly bears in the region based on long-term movements of bears. Identifying possible sub-populations of grizzly bears in the central Arctic may be important for effective management of bears in the area. For example, using mark-recapture data to enumerate a population often requires knowledge of immigration and emigration rates to satisfy assumptions of population closure (Otis et al. 1978; Krebs 1989), or to correct abundance estimates. Modelling population growth and setting sustainable harvest levels also may require knowledge of immigration or emigration rates to be accurate. Rates of immigration and emigration for a

population, however, can be determined only if bounds delineating a population are known. Estimates of abundance and demographic rates of wildlife populations may thus require knowledge of population boundaries to be reliable.

The spatial organization of barren-ground grizzly bears in the central Arctic is currently unknown. Two hypotheses can be stated which represent extremes on a continuum scale. On the one hand, grizzly bears may exhibit home ranges with limited overlap among members of the same sex, as reported for populations inhabiting mountainous environments (e.g., Mace and Waller 1997). If true, population delineation of grizzly bears could be linked to broad habitat features that underline bear distribution, or based on large-scale management boundaries (e.g., hunting zones, mining claim blocks). On the other hand, grizzly bears may exhibit extensive seasonal movements in order to exploit spatially available food resources (e.g., migrating caribou). In this case, the spatial structure of grizzly bear populations would be apparent only over a very large scale (>500 km), as recently reported for polar bears (Bethke et al. 1996; Taylor et al. 2000).

Presently, Wildlife Management Zones and Grizzly Bear Management Areas in Nunavut and the Northwest Territories likely do not lend themselves to the effective management of grizzly bears in the central Arctic (Government of the Northwest Territories, 1991, Discussion paper towards the development of a Northwest Territories barren-ground grizzly bear management plan, Yellowknife, Northwest Territories, Canada). Current areas of grizzly bear management are based on muskox (*Ovibos moschatus*) management zones that were already established in the vicinity of coastal communities. These areas probably do not allow for a

complete evaluation of the pressures exerted by some communities on grizzly bears, or reflect grizzly bear distribution, movements, habitat, and perhaps harvest patterns. If management of grizzly bears in the central Arctic is to be effective, the existence of any geographically distinct sub-populations in the region should be properly delineated. Further, demographic rates and abundance estimates for grizzly bears in the central Arctic will be obtained in the near future; such estimates will likely rely on scientifically-based estimations of population boundaries for technique and accuracy. The objective of Chapter 2 of this thesis was to identify spatial groups of grizzly bears in the central Arctic that could be considered independent populations for management purposes.

1.2.2 Hierarchical Habitat Selection by Barren-Ground Grizzly Bears in the Central Arctic

The use an animal makes of habitats in its environment is central to animal ecology. Habitat selection affects all subsequent choices of food items or other resources necessary for survival and reproduction. The selection of habitats in the environment should thus reflect the quality of those habitats in terms of promoting survival and reproduction (Levins 1968). Organisms will select habitats in which their survival and reproductive success is high. Organisms that select less profitable habitats will have lower survival and contribute fewer offspring to future generations. Identifying preferred habitats by animals is therefore fundamental to the understanding of the relationship between animals and their environment. The objective of Chapter 3 of this thesis was to examine the habitat selection patterns of

grizzly bears in the central Arctic in order to better understand the relationship between barren-ground grizzly bears and the tundra environment.

Ecologists are now aware that study conclusions may depend on the spatial or temporal scale of observation (Allen and Starr 1982; O'Neill et al. 1986; Wiens 1989; Duarte 1991; Levin 1992; Allen and Hoeskstra 1993). Ecological variability can be viewed as structured in a nested array of scales of variation, each contributing part of the global variability and presenting patterns that may differ from level to level (Duarte 1991). The selection of habitats by animals, too, can be viewed as a hierarchical process. For example, Johnson (1980) identified four spatial scales of habitat selection. Adhering to the fundamentals of hierarchy theory (Allen and Starr 1982; O'Neill et al. 1986; O'Neill 1989; Allen and Hoeskstra 1993), these spatial scales of habitat selection correspond to different rates of selection processes. First order selection is the selection of the physical or geographic range of a species, and may be determined over periods of evolutionary time. Second order selection determines the home range of an individual within the geographic range of the species, and is determined over the lifetime of an animal. Third order selection determines feeding sites within the home range that may be selected on a daily or hourly basis. Fourth order selection is defined by foraging decisions like prey choice or choice of browse within a feeding site. These decisions may be made on a minute-by-minute or even second-by-second basis.

In Chapter 3, I assess the habitat selection patterns of grizzly bears in the central Arctic using resource selection functions (Manly 1993; Boyce and McDonald 1999) at two scales: Johnson's (1980) second and third orders of selection. At the

second order of selection I compare the availability of habitat types in the home ranges of grizzly bears to the availability of habitat types in the study area (Roy and Dorrance 1985; Thomas and Taylor 1990). At the third order of selection I compare the proportional use of habitat types within a bear's home range to the proportional availability of habitat types within available sections of the home range. Here, buffers around individual telemetry locations are used to determine proportional use of habitat types (Rettie and McLoughlin 1999; Rettie and Messier 2000). Further, I employ the relatively recent method of varying the area available for habitat use from one location to the next according to the amount of elapsed time between successive telemetry locations (Arthur et al. 1996).

1.2.3 Effect of Temporal and Spatial Differences in Habitat on Home Ranges of Barren-Ground Grizzly Bears in the Central Arctic

In Chapter 4 of this thesis I describe the home ranges of grizzly bears in the central Arctic and assess the importance of habitat as a determinant of home range size. I conduct my assessment at two levels: 1) the individual level, which compares the size of home ranges across individuals within a single population; and, 2) the population level, which compares the average home range size among populations within the same species (McLoughlin and Ferguson 2000). Within the population of grizzly bears in the central Arctic I examine the effects of both temporal and spatial differences in habitat on home range size. To understand temporal fluctuations in movement patterns, I describe changes in the seasonal ranges of grizzly bears in the central Arctic. To assess the effect of spatial differences in habitat on home range

size I explore relationships between proportional availabilities of habitat types within the home ranges of grizzly bears in this study and range size. I hypothesize that if bears are responding to the availability of different habitats in the environment, home ranges should vary with the proportional availability of habitat types within the home range. For example, home ranges may increase as the proportion of habitats in the home range that provide poor food value to bears increases, or as quality habitats become more patchily distributed within a matrix of poorer quality habitats. At the level of the population I further examine the effects of spatial differences in habitat on home range size. I test a possible explanation for why the mean annual ranges of barren-ground grizzly bear populations are generally larger than interior and Pacific-coastal populations of grizzly bears. I hypothesize that bears have responded to low primary productivity in Arctic tundra environments with large ranges to obtain adequate food resources.

1.2.4 Denning Ecology of Barren-Ground Grizzly Bears in the Central Arctic

Recent discoveries of diamond-bearing kimberlite pipes in the central Arctic have led to intense exploration activity and the development of the first of likely several diamond mines. Plans to develop the region include the construction of several all-weather roads and infrastructures requiring granular materials from eskers, kames, and drumlins. Composed mainly of sand and gravel, eskers and related surface expressions are prominent topographic features that trace the path of collapsed depositional landforms (e.g., glacial rivers) due to melting of supporting ice (Soil Classification Working Group 1998). Previous studies in the central Arctic

(Mueller 1995; Banci and Moore 1997) suggested that esker habitat was extremely important to barren-ground grizzly bears, wolves (*Canis lupus*), Arctic ground squirrels (*Spermophilus parryi*), and foxes (*Vulpes vulpes* and *Alopex lagopus*) for denning. The use of granular materials by industry may therefore present a problem for the conservation of wildlife possibly reliant upon glacio-fluvial habitats for denning, including barren-ground grizzly bears.

To mitigate possible conflicts between industry and the conservation of grizzly bears in the central Arctic, the extent to which bears rely on eskers and related features for denning needs to be established. Unfortunately, previous studies of the denning habits of grizzly bears in the central Arctic (e.g., Mueller 1995; Banci and Moore 1997) have not been able to clearly answer this question, partly due to biases in methods of data collection. For example, both Mueller (1995) and Banci and Moore (1997) relied upon aerial and ground surveys of dens of unknown bears to collect data on denning habits, but biased their studies by spending most of their time surveying esker habitat for bear dens. Esker habitat, however, represents only ~1.5% of the landscape in the central Arctic. Further, bear dens are much easier to identify from the ground or air if excavated in open esker habitat compared to more heavily-vegetated habitats, such as tall shrub riparian areas. It is not surprising that both Mueller (1995) and Banci and Moore (1997) claimed that eskers were extremely important for grizzly bear denning relative to other habitats. These claims, however, must be interpreted with caution, and a re-evaluation of the importance of eskers to grizzly bear denning is required before conservation recommendations to preserve esker habitat for grizzly bear denning can be effectively argued.

In Chapter 5 of this thesis I re-evaluate the importance of eskers and other habitats as denning habitat for barren-ground grizzly bears in Canada's central Arctic. I document the denning habits of grizzly bears in the central Arctic by following satellite and VHF radio-collared bears to their dens. By using telemetry to collect data on denning habits, I eliminate some of the biases associated with aerial and ground surveys of dens of unknown bears. I quantify the importance of esker habitat and other habitats for denning by bears and document den characteristics of recently excavated dens. Further, telemetry data allowed me to examine when grizzly bears entered and exited dens. Data on denning chronology has not previously been reported for grizzly bears in the central Arctic.

1.2.5 General Discussion and Management Implications

In Chapter 6, I explore important topics concerning the spatial organization and habitat selection patterns of grizzly bears that are not fully discussed in previous chapters. I present a conceptual model for the spatial organization of solitary, food-maximizing organisms (McLoughlin et al. 2000) that helps explain the evolution of spatial organization in grizzly bears of the central Arctic. I then re-visit the importance of acknowledging scale dependence in habitat selection, and apply that premise to the novel application of using resource selection functions to estimate animal abundance (Boyce and McDonald 1999). Finally, I present management implications of research contained in this thesis for the conservation of barren-ground grizzly bears in the central Arctic.

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2. POPULATION DELINEATION OF BARREN-GROUND GRIZZLY BEARS IN THE CENTRAL ARCTIC

2.1 Introduction

Using mark-recapture data to enumerate a population may require knowledge of immigration and emigration rates to satisfy assumptions of population closure (Otis et al. 1978; Krebs 1989) or to correct abundance estimates. Modelling population growth and setting sustainable harvest levels also may require knowledge of immigration or emigration rates to be accurate. Rates of immigration and emigration for a population, however, may only be determined if bounds delineating a population are known. Estimates of abundance and demographic rates of wildlife populations may thus require knowledge of population boundaries to be reliable.

If wildlife populations are restricted in movement by natural geographic boundaries or habitat fragmentation, then population delineation could be linked to relatively broad habitat features. For example, park boundaries, reserve boundaries, mountain ranges, forests, watersheds, and lakes may be used to identify the bounds of insular populations. It is more difficult, however, to define population boundaries for free-ranging species that are neither restricted by natural geographic boundaries nor habitat fragmentation.

Recently, Bethke et al. (1996) introduced a method by which geographically distinct populations of free-ranging polar bears (*Ursus maritimus*) in the Canadian Arctic could be delineated using radio-telemetry data and multivariate cluster analysis. The approach is to test for the presence of spatial clusters of animals based on movement data. Then, using a home range estimator, one can identify the geographic range of populations for management purposes. The procedure may hold promise for researchers wishing to identify population ranges of species that are unrestricted by natural or artificial boundaries and possess continuously overlapping home ranges.

Barren-ground grizzly bears (*Ursus arctos*) inhabiting Canada's central Arctic (Chapter 1; Fig. 1.1) are unrestricted in their movements by topography or human development. Grizzly bears in the region possess some of the largest ranges yet reported for grizzly bears in North America (McLoughlin et al. 1999; Chapter 4). Further, home range overlap for bears in the area is also relatively high (McLoughlin et al. 2000; data on file). The population delineation procedure of Bethke et al. (1996) may thus be applicable for delineating possible sub-populations of grizzly bears in the central Arctic for management purposes.

Presently, Wildlife Management Zones and Grizzly Bear Management Areas in Nunavut and the Northwest Territories likely do not lend themselves to the effective management of barren-ground grizzly bears in the central Arctic (Government of the Northwest Territories, 1991, Discussion paper towards the development of a Northwest Territories barren-ground grizzly bear management plan, Yellowknife, Northwest Territories, Canada). Current areas of grizzly bear

management are based upon muskox (*Ovibos moschatus*) management zones that were already established in the vicinity of coastal communities. These areas probably do not allow for a complete evaluation of the pressures exerted by some communities on grizzly bears, or reflect grizzly bear distribution, movements, habitat, and perhaps harvest patterns. If management of grizzly bears in the central Arctic is to be effective, the existence of any geographically distinct sub-populations in the region should be properly delineated. Further, demographic rates and abundance estimates for grizzly bears in the central Arctic will be obtained in the near future; such estimates will likely rely on scientifically-based estimations of population boundaries for technique and accuracy.

The objective of this Chapter was to identify spatial groups of grizzly bears in the central Arctic that could be considered independent populations for management purposes. Here, the term population is used not to refer to populations or sub-populations in a genetic sense, but rather to identify a demographic unit for which population growth rate is determined largely by intrinsic birth and death rates, and not immigration or emigration. I applied the methods of Bethke et al. (1996) to describe the spatial organization of grizzly bears in the central Arctic.

2.2 Methods

2.2.1 Study Area

The study area was located in Canada's central Arctic, encompassing approximately 235,000 km^2 of mainland Nunavut and the Northwest Territories

(Chapter 1, Fig. 1.1). The study area was delineated, clockwise, by the community of Kugluktuk, the Kent Peninsula, Aylmer Lake, Mackay Lake, and Great Bear Lake. The region is characterized by short, cool summers and long, cold winters. Summer temperatures average 10°C and winter temperatures are commonly below -30°C; the area is semi-arid with annual precipitation around 300 mm, about half of which falls as snow (BHP Diamonds Inc., 1995, Ecological mapping: 1995 baseline study update, Yellowknife, Northwest Territories, Canada). Drainages support willow (*Salix* spp.) and dwarf birch (*Betula glandulosa*) shrubs as tall as 3 m, and birch shrublands (<0.5 m in height) dominate the uplands. Shrubs such as blueberry (*Vaccinium uliginosum*), cranberry (*Vaccinium vitis-idaea*), and crowberry (*Empetrum nigrum*) are common and their berries are important foods to grizzly bears (Gau 1998). The Bathurst caribou (*Rangifer tarandus*) herd migrates annually through the study area. The herd leaves wintering grounds below the treeline in April, travels to calving grounds near Bathurst Inlet by early June, and disperses south in late summer and autumn. The herd was estimated at 349,000 ± 95,000 caribou >1 year of age in 1996 (Gunn et al. 1997). Muskox occur locally in the northern half of the study area. Much of the study area is part of a well-drained peneplain with lakes in the hollows and scattered depressions. Rounded rocky hills and glacio-fluvial features such as eskers, kames, drumlins, and raised beaches are often the only major relief features.

2.2.2 Animal Capture and Telemetry

The population delineation method of Bethke et al. (1996) requires that sampling of individuals for movement data be uniformly distributed throughout a study area. This was attempted here as much as possible.

I used satellite radio telemetry (Service Argos Inc., Landover, Maryland, USA) to obtain movement data on barren-ground grizzly bears. Satellite telemetry provides continued and precise (approximately ±0.5 km, SD) information on bear movements with minimum disturbance to bears (Fancy et al. 1988; Harris et al. 1990). Satellite collars (Telonics, Mesa, Arizona, USA) were equipped with a VHF beacon to permit relocations of radio-marked animals from an aircraft and, eventually, for the retrieval of collars. Most collars were designed to transmit approximately two to five locations every two days (eight-hour duty cycle) from 1 May–1 November. During other months, collars were programmed to transmit locations every eight days to minimize output of battery power.

Between May 1995 and June 1999, myself and field crews used a Bell 206B or Hughes 500 helicopter to search for and capture bears. A Piper SuperCub or Aviat Husky aircraft equipped with skis or floats was sometimes used for more intensive searches of the study area. Most grizzly bears were captured in spring during the snow melt period (15 May–5 June) by following tracks in the snow. We immobilized each bear with an injection of titelamine hydrochloride and zolazepam hydrochloride (Telazol®, Ayerst Laboratories Inc., Montreal, Quebec, Canada) from a projected dart. Immobilized animals were marked with identification numbers applied as ear tags and permanent lip tattoos. Bears were weighed using a load-cell scale (Norac

Systems International Inc., Saskatoon, Saskatchewan, Canada) while suspended in a cargo net from a helicopter. We measured heart girth, straight-line body length, skull length, and skull width with a tape measure and calipers, and extracted a vestigial premolar tooth for age determination (Craighead et al. 1970). Some bears were tested for nutritional condition using bioelectrical impedance analysis and blood sampling (Gau 1998). Only those bears weighing >110 kg (males) and >90 kg (females) were fitted with satellite radio-collars before release.

2.2.3 Cluster Analysis

In order to use satellite relocations in a cluster analysis, the latitude-longitude coordinate system upon which relocations are based must first be scaled to a common *x-y* grid (Bethke et al. 1996). A geographical information system (SPANS® Explorer™ 7.0, Tydac Research Inc., Nepean, Ontario, Canada) was used to convert bear relocations to Lambert grid coordinates to yield a "meters easting" and "meters northing" coordinate system, and formed the basis for all other spatial analyses described herein. The *x-y* Lambert grid was based upon a Lambert Conformal Conic projection covering the entire study area.

For each grizzly bear, a median meters easting value and a median meters northing value for each of four seasons in a year were calculated from movement data, and placed in a data matrix (bear × season) upon which cluster analysis could be performed. I stratified the data matrix by season to account for seasonal variations in range size and movement rates (McLoughlin et al. 1999; Chapter 4). I defined seasons according to changes in the diet of barren-ground grizzly bears during the

active period (adapted from Gau 1998), including: spring (den emergence–20 June), summer (21 June–31 July), late-summer (1 August–9 September), and autumn (10 September–den entrance). Den emergence generally occurs in the last week of April and den entrance in the last week of October (Chapter 5). Only those individuals that transmitted in all seasons of the year were included for analysis; however, if an individual transmitted locations in three out of four seasons, and there was a location recorded within one week from one of the bracketing seasons, the closest location from the bracketing seasons was used as an observation for the missing season (Taylor et al. 2000). I treated animals with two or more years of consecutive seasons as separate observations (i.e., I used bear-years as the sampling unit).

Because of known differences in the range requirements and seasonal movement rates between sexes (McLoughlin et al. 1999; Chapter 4), I conducted separate cluster analyses for males and females. Previous analyses using the method of Bethke et al. (1996) were conducted only for female animals (e.g., Bethke et al. 1996, Taylor et al. 2000); however, the movement patterns of both males and females will determine the spatial continuity of a breeding population. Here, the clustering of both female and male movement patterns were used for the final interpretation of population continuity in the central Arctic.

For each sex I used agglomerative hierarchical cluster analysis to group objects (bears) according to similarity (Pielou 1984; Romesburg 1984). Analyses were performed using SPSS 10.0 for Windows (SPSS Inc., Chicago, Illinois, USA). The unstandardized matrix of objects (bears) and attributes (seasonal median x and y coordinates) were used to calculate the values of the Euclidean distance or

resemblance coefficient. I used Ward's minimum variance technique (Pielou 1984; Romesburg 1984) to process the values of the resemblance coefficient to create a dendrogram that shows the hierarchy of similarities among all pairs of objects (bears). The interpretation of clusters was based on a hierarchical separation of objects into a small number of definable groups ($n = 3$).

2.2.4 Mapping Population Boundaries

I assigned individuals to "populations" based upon cluster analysis results. For any given sex and population, bear locations were pooled and then used in a home range analysis to map the spatial distribution of the population. I analyzed the *x-y* coordinate data to detail the spatial distribution of populations using the fixed kernel technique with least squares cross-validating (LSCV) to determine bandwidths (Silverman 1986; Worton 1989*a*,*b*, 1995; Seaman and Powell 1996). I calculated population ranges using the program "The Home Ranger", Version 1.1 (F. W. Hovey, British Columbia Forest Service, Research Branch, Columbia Forest District, P.O. Box 9158, R.P.O. No. 3, Revelstoke, BC V0E 3K0, Canada). I plotted utilization distribution contours (90% and 70%) for population ranges in SPANS GIS. I then used the contours to guide placement of population boundaries. Where possible, I used a single boundary to delineate the population range of both male and female clusters. In areas where there was broad overlap in low-use areas (>70% contour level) several boundary lines were possible. Here, I used political boundaries to place population unit boundaries (Bethke et al. 1996).

2.2.5 Validating Population Boundaries

I used two criteria to validate populations identified by cluster analysis and to then delineate population boundaries using home range analysis. I hoped to define resident breeding populations; thus, to validate population units, I first required that spatial clusters for male and female bears be similar enough in distribution such that both distinctive male and female components could be contained within identifiable population boundaries (70% contour level). Second, to ensure that population growth rates for identified populations would be determined largely by intrinsic rates of birth and death, and not immigration or emigration, I required that no more than one radio-tracked animal of either sex could immigrate to or emigrate from a population unit annually. Even allowing one animal to immigrate to or emigrate from a population unit permitted a generous annual population exchange rate (between 2.1% and 4.3% of a given population per year). I determined immigration and emigration rates by analyzing the movements of all independent bears captured in the study for each year in which a bear was observed. Exchange for an individual was considered to have taken place if an animal moved from the population in which it either emerged from its den or was captured in the early part of one year to another population as determined by where the bear emerged from its den in the following year. I considered data for each "bear-year"—the period from one spring to the next during which data for a bear were collected—to represent an independent sample. Annual exchange among populations was thus based on the entire collection of several years of bear movement data. By limiting the calculation of exchange rates to where individuals moved from the early part of one year to the next, I hoped to further

define identified populations as breeding populations. Grizzly bears in the study area generally breed from shortly after den emergence through early summer (*personal observation*).

2.3 Results

2.3.1 Animal Capture and Telemetry

Eighty-one barren-ground grizzly bears (n = 42 females, n = 39 males) were captured and equipped with satellite radio-collars in the study area (Fig. 2.1), yielding a total of 8,054 locations (n = 4,370 for females, n = 3,684 for males) and 96 bear-years of data (n = 55 for females, n = 41 for males) for use in this study. Movement patterns for males and females are indicated in Figs. 2.2 and 2.3. Individual annual ranges averaged 2,100 km^2 for adult females and 7,200 km^2 for adult males (Chapter 4). Subadult males ranged from ~10,000 km^2 to ~40,000 km^2 in a single year (data on file).

2.3.2 Cluster Analysis

The dendrogram obtained for females presented three population clusters (Fig. 2.4): a cluster in the North Slave area, Bathurst Inlet area, and Kugluktuk area (Fig. 2.5). The utilization distribution contours indicated marginal overlap of population ranges (Fig. 2.5).

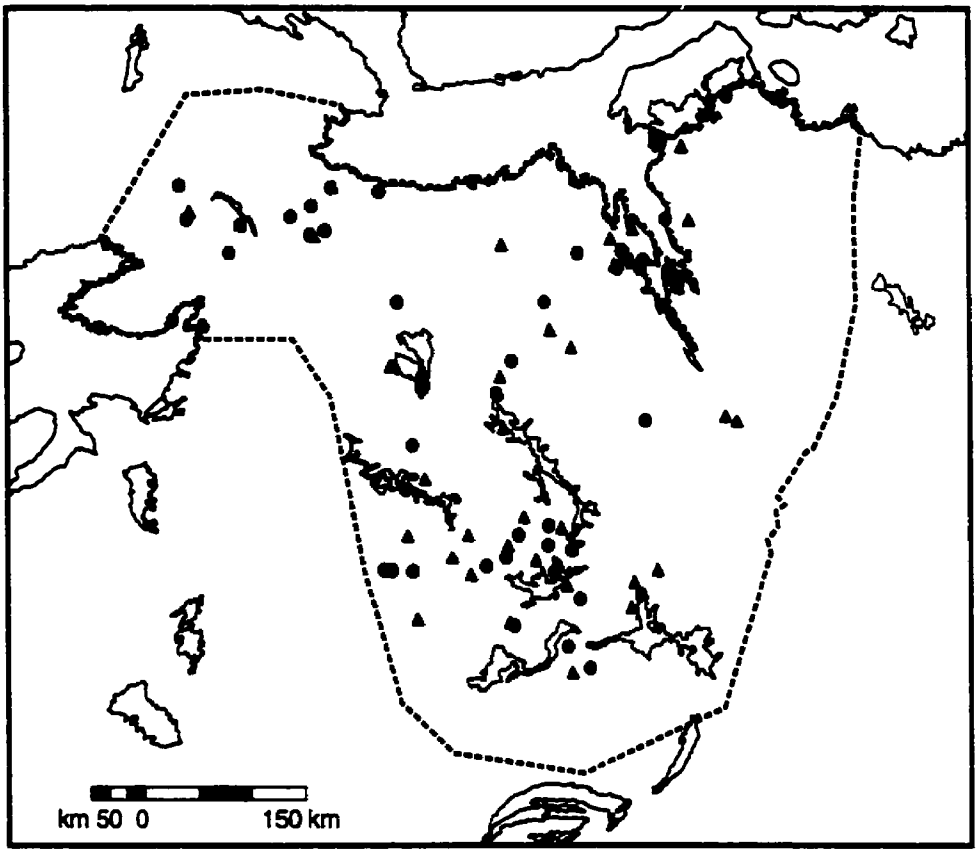

Fig. 2.1. Distribution of grizzly bear capture locations for satellite radio-collar deployment in the central Arctic, 1995–1999. Circles represent capture sites of females, triangles represent capture sites of males. Study area bounds are indicated by the hatched line.

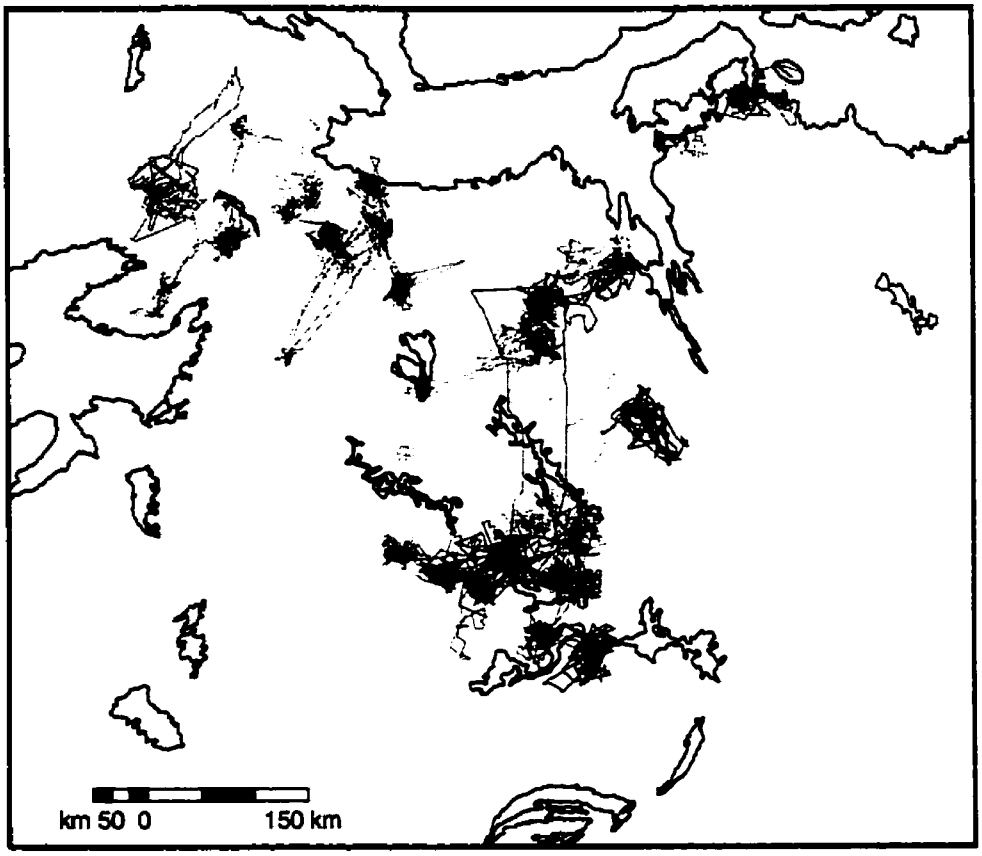

Fig. 2.2. Multiannual movements of female grizzly bears in the central Arctic, 1995–1999. Movements of individuals are presented as different shades of grey.

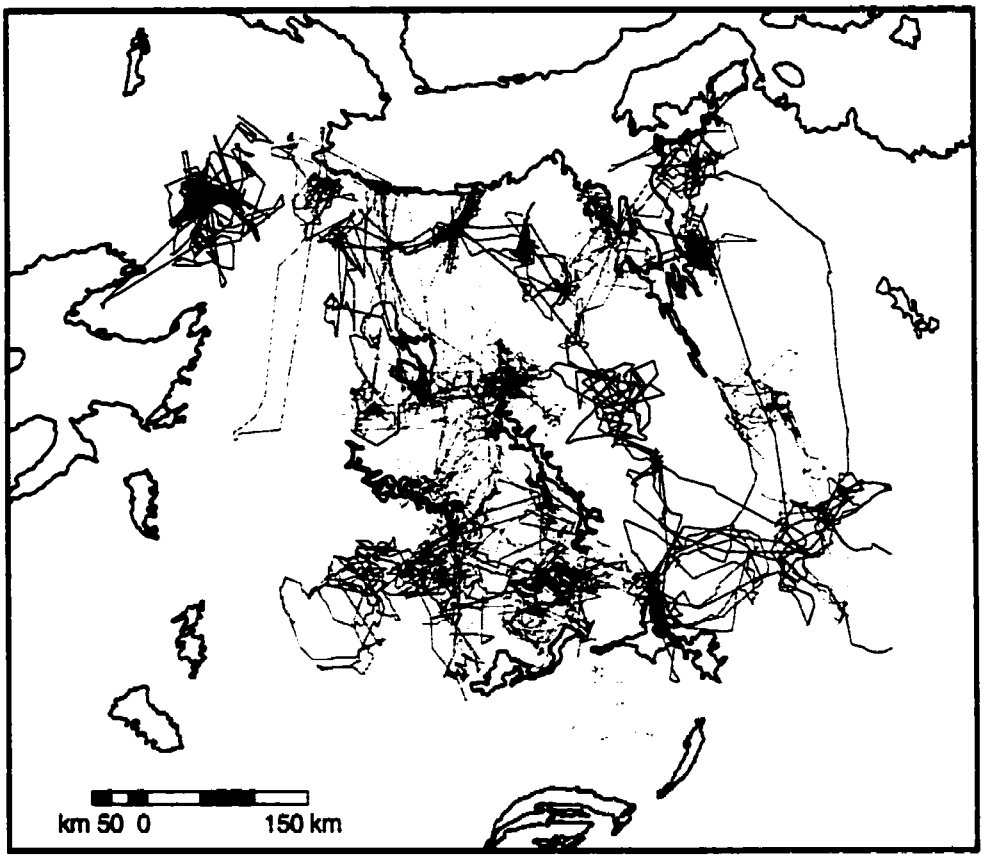

Fig. 2.3. Multiannual movements of male grizzly bears in the central Arctic, 1995–1999. Movements of individuals are presented as different shades of grey.

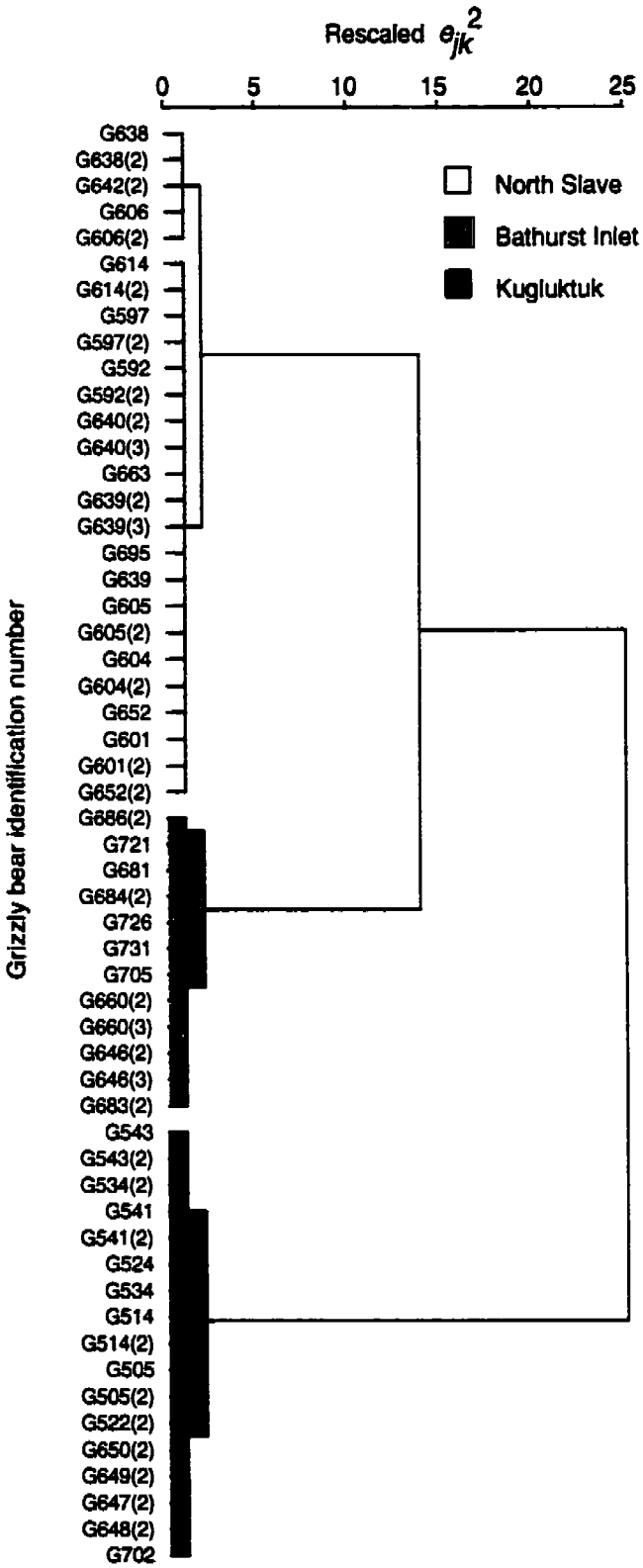

Fig. 2.4. Dendrogram showing spatial clusters of female grizzly bears in the central Arctic. Objects (bears) were based on one bear-year of movement data.

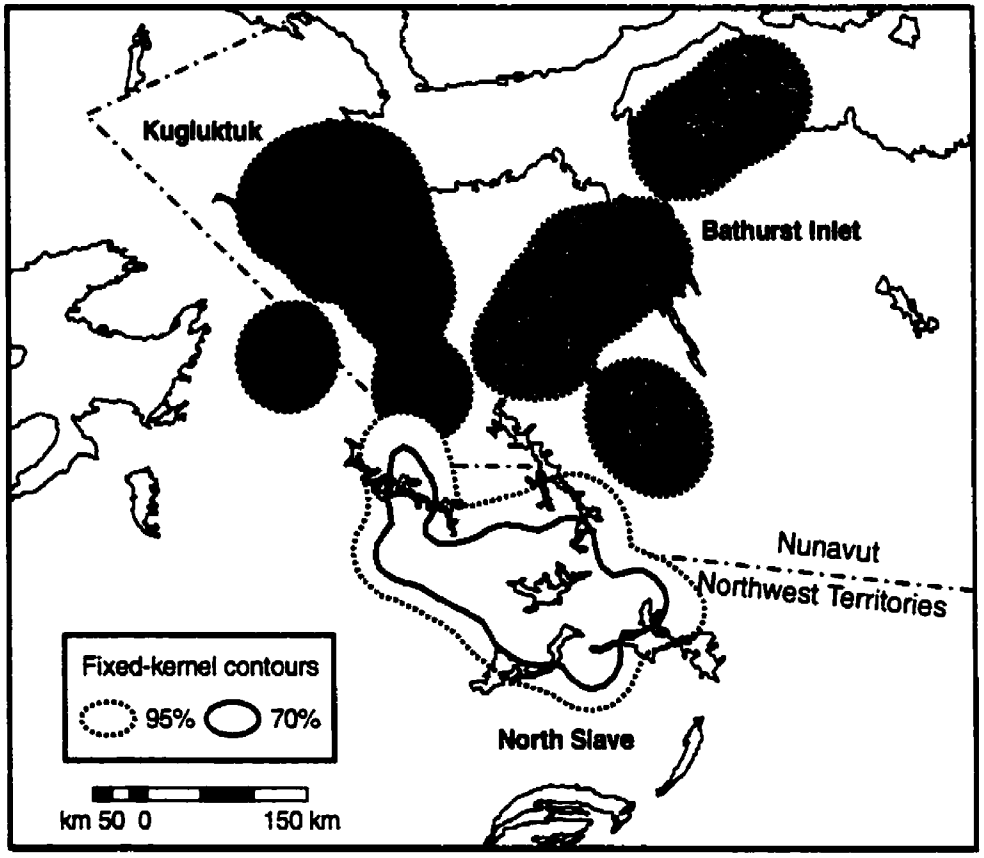

Fig. 2.5. Utilization distributions (fixed kernel contours) for the North Slave, Bathurst Inlet, and Kugluktuk clusters for female grizzly bears in the central Arctic.

Like the analysis for females, the dendrogram obtained for males indicated a separation of bears into approximately three clusters (Fig. 2.6). The three identified populations were located in similar areas as the female population ranges: the North Slave area, Bathurst Inlet area, and Kugluktuk region (Fig. 2.7). Unlike for females, however, population ranges for male grizzly bears indicated higher overlap (Fig. 2.7), even at the 70% utilization contour level.

2.3.3 Mapping Population Boundaries

I set population boundaries based on the 70% utilization contours for female and male clusters. Identified populations included the North Slave unit, Bathurst Inlet unit, and Kugluktuk unit (Fig. 2.8). The political border separating Nunavut from the Northwest Territories was used to separate the North Slave unit from the Kugluktuk and Bathurst Inlet units, as the 70% contours showed no overlap among female clusters. Marginal overlap of the male population clusters occurred at the 70% contour level, however. The Nunavut/Northwest Territories border was also used to enclose the western perimeter of the Kugluktuk unit, separating that unit from the Sahtu Settlement Area of the Northwest Territories (Fig. 2.8).

2.3.4 Validating Population Boundaries

Movement data (1995–1999) from a total of 102 bear-years ($n = 61$ for females, $n = 41$ for males) were analyzed to determine expected annual exchange

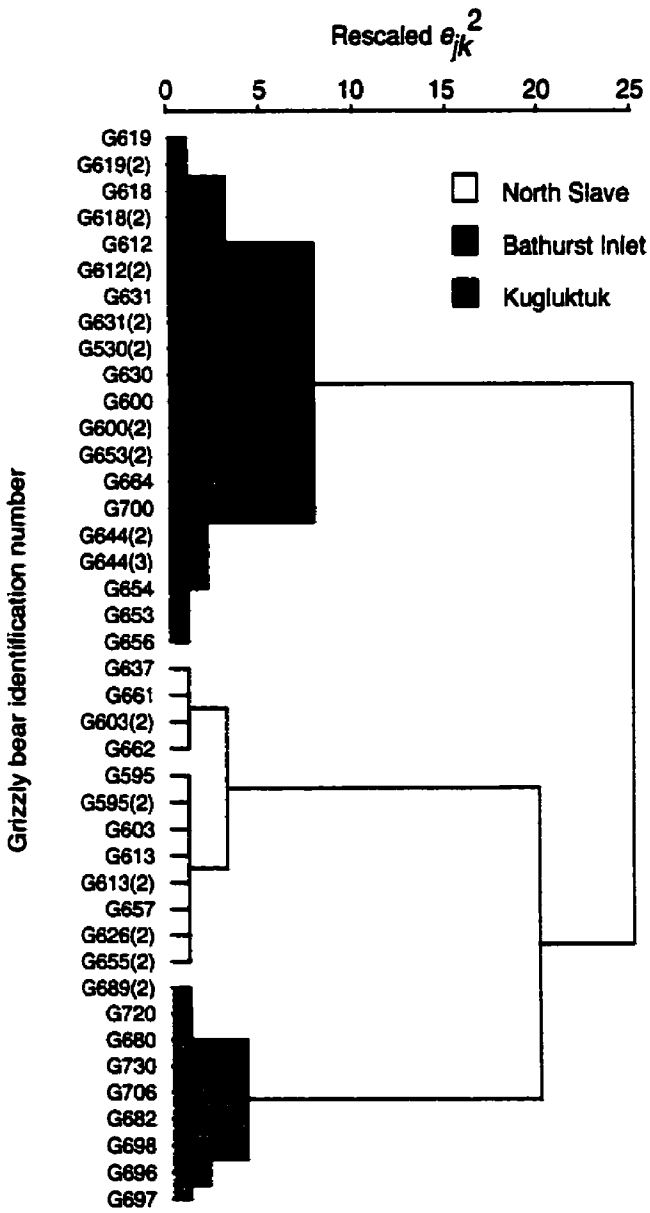

Fig. 2.6. Dendrogram showing spatial clusters of male grizzly bears in the central Arctic. Objects (bears) were based on one bear-year of movement data.

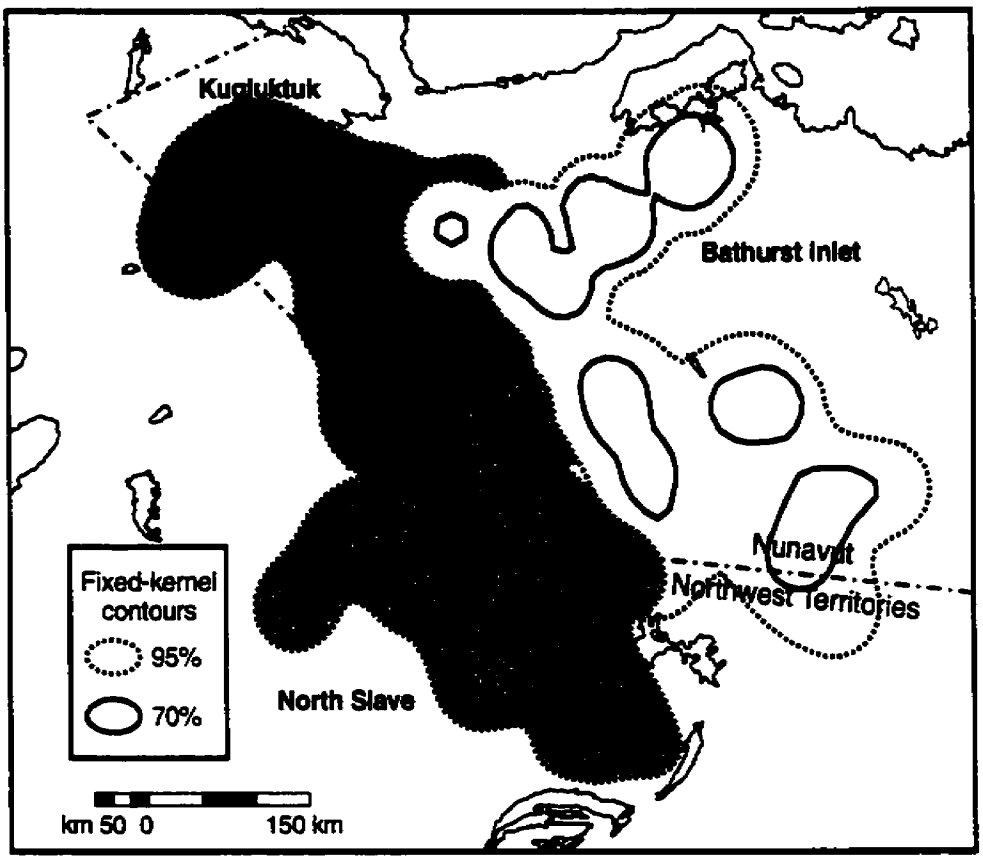

Fig. 2.7. Utilization distributions (fixed kernel contours) for the North Slave, Bathurst Inlet, and Kugluktuk clusters for male grizzly bears in the central Arctic.

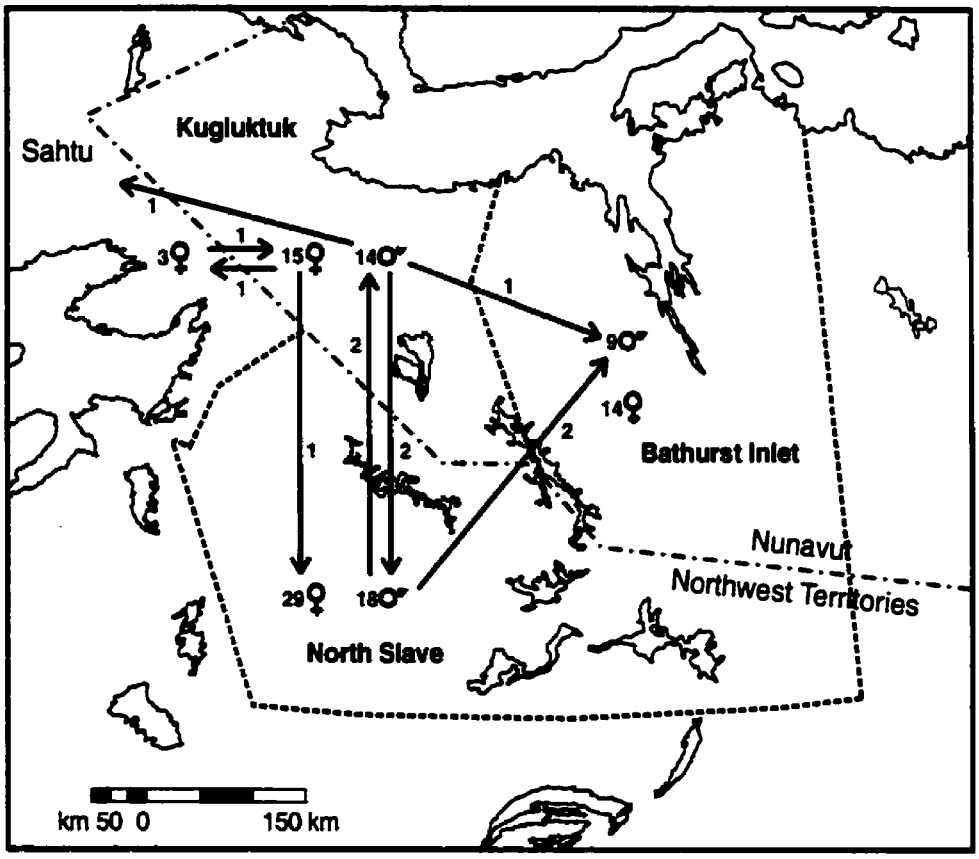

Fig. 2.8. Final boundaries of grizzly bear populations for the North Slave, Bathurst Inlet, and Kugluktuk clusters in the central Arctic. Boundaries were based on the 70% utilization distributions (fixed kernel) for male and female populations. Immigration and emigration after one bear-year of data (see text) are indicated for the female and male components of each population unit. Arrows indicate direction of exchange and number and sex of animals immigrating or emigrating across population boundaries. Numbers next to gender symbols indicate the number of resident bears of a sex originating in a population unit.

among identified populations (Fig. 2.8). After one year, one of 17 adult female bears that originated in the Kugluktuk area moved into the North Slave unit. Another female from the Kugluktuk unit emigrated across the Nunavut/Northwest Territories border into the Sahtu Settlement Area of the Northwest Territories. I recorded movements of this same female back into the Kugluktuk unit a year later. And, after one year, two of 14 male bears emigrated from the Kugluktuk unit to the North Slave unit. From the Kugluktuk unit a further two males emigrated to the Bathurst Inlet unit, and another male emigrated across the Nunavut/Northwest Territories border into the Sahtu Settlement Area. Also, after one year, two of 18 males emigrated from the North Slave area to the Kugluktuk unit. Another male of the North Slave population unit moved to the Bathurst Inlet unit. No bears were observed to emigrate from the Bathurst Inlet population unit, although three males immigrated to this region.

2.4 Discussion

If geographic bounds for a population can be clearly established, population size, demographic rates, and life-history parameters may be estimated with greater reliability from accurate estimates of immigration and emigration rates. Further, a greater number of methods are available to enumerate a closed (where births, deaths, immigration, and emigration are assumed to be zero), rather than open (no assumptions of demographic rates), population (Krebs 1989). If geographic bounds for a population cannot be established, then estimates of demographic rates must be

obtained with discretion, and techniques of abundance estimation must be restricted. For example, the Cormack-Jolly-Seber technique (see Krebs 1989) is the only mark-recapture method available to enumerate open populations; several other enumeration techniques are available if rates of immigration and emigration can be assumed to be zero (e.g., Lincoln-Peterson, Schnabel methods, Otis et al. 1978; Krebs 1989). The degree of connectivity within a population or among two or more identified populations will also have important ramifications for how a given population is best managed. For example, if harvest rates are set for a population that is continuous with a neighbouring population or management unit, animals from both areas may be affected jointly. This could pose a conservation problem if population connectivity is not recognized, particularly if the two areas of management are isolated politically (e.g., divided by the borders of two countries, states, provinces, or territories).

I tested the connectivity of the barren-ground grizzly bear population in the central Arctic, an area bisected by a territorial border. Here, for identified population units to be valid, I required that population units contain both distinctive male and female components as determined by the independent clustering of male and female bears in the study area. Further, I required negligible exchange of individuals among identified population units. The latter criteria was to ensure that spatial closure of population units was such that demographic processes within a unit would be mainly a function of intrinsic birth and death rates, and not immigration or emigration rates (i.e., independent demographic units).

My first validation rule was at least partially satisfied. I obtained independent clustering solutions that grouped both male and female grizzly bears into three

relatively distinct areas: the North Slave region, Bathurst Inlet region, and Kugluktuk region. Spatial clusters for male and female bears appeared similar enough in distribution so that distinctive male and female components could be contained within common population boundaries. Matches between male and female ranges for a population unit were not perfect, however. Although female population ranges were completely contained within established population unit boundaries at the 70% contour level, male population ranges demonstrated a higher degree of overlap. Due to this overlap, no population range for males could be completely contained within a designated population boundary. From these results it was anticipated that population closure would be less than that needed to designate population units as independent demographic units.

Exchange rates among population units implied poor population closure. And, not surprisingly, this was more evident for the male, rather than the female, constituent of population units. In any given year, 35% of the males in the Kugluktuk area could be expected to emigrate annually from the population unit (14% each to the North Slave and Bathurst Inlet units, 7% to the Sahtu Settlement Area). Immigration to the Kugluktuk unit may potentially be 14%. Also, after one year, 22% of the males in the North Slave unit could potentially move out of the population unit (11% each to the Kugluktuk and Bathurst Inlet units). Immigration of males may potentially be 11%. No males were observed to emigrate from the Bathurst Inlet population unit, but immigration to the region could be 18% annually.

Although not generally as high as for males, females also demonstrated population exchange. The fact that female exchange occurred among population units

is important. In a polygonous species such as the grizzly bear, provided there are enough males to mate all receptive females in a population, the intrinsic rate of increase of females will likely determine the population's intrinsic rate of increase (Caughley 1977: 133). Population growth rates may thus be affected more by female exchange than male exchange. Here, female immigration to the Kugluktuk unit may potentially be 7%/year, and emigration from the Kugluktuk unit may potentially be 13%/year. Female immigration to the North Slave unit may be 3.4% annually. Considering data from both sexes, but especially from females, leads me to conclude that exchange among units was higher than that required to identify any of the three populations as independent demographic units. At least, population closure at the genetic level cannot be assumed due to immigration and emigration rates.

In addition to the above, several males and females spent long periods of time (>2 weeks) in population units other than those from where they originated, but returned to their population of origin to den. During these periods it was possible for several of these animals to mate (I have seen matings as late in the year as July 25); however, exchange for these bears was not calculated. These findings further imply an open (continuous), rather than closed, population of barren-ground grizzly bears in the central Arctic.

The data also suggest that the Nunavut portion of the Kugluktuk cluster is continuous with the Sahtu Settlement Area immediately west of the Nunavut/Northwest Territories border and north of the North Slave population unit. I documented three cases of exchange across this border (two female, one male). Further, one female that clustered in the Kugluktuk area was captured in and denned

exclusively in the Sahtu Settlement Area. Although this female did not demonstrate emigration as defined in the methods of this study, she did, however, spend large amounts of time (>1 month/year) on the Kugluktuk side of the territorial border. I could not test whether bears of the Bathurst Inlet area were continuous with those bears ranging east to Hudson's Bay, or whether bears of the North Slave unit were continuous with those bears that range south and west of the treeline. Based on results obtained for bears within the central Arctic, however, it is likely that bears in the North Slave and Bathurst Inlet units are continuous with adjacent bear populations located outside the study area.

The grizzly bear population in the central Arctic should be treated as an open (continuous) population. The study area may still be divided and managed along the population boundaries identified herein for logistical and political reasons; however, it must be realized that management practices implemented in one identified unit will likely affect adjacent units. In addition, the bear population in the study area is likely continuous with bear populations located adjacent to and outside the study area. Techniques of estimating population abundance for grizzly bears in the central Arctic should be restricted to those that do not assume population closure (e.g., Cormack-Jolly-Seber method, Krebs 1989; through the use of resource selection functions, Boyce and McDonald 1999).

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3. HIERARCHICAL HABITAT SELECTION BY BARREN-GROUND GRIZZLY BEARS IN THE CENTRAL ARCTIC

3.1 Introduction

The use an animal makes of its environment is central to animal ecology. Habitat selection affects all subsequent choices of food items or other resources necessary for survival and reproduction. The selection of habitats in the environment should thus reflect the quality of those habitats in terms of promoting survival and reproduction (Levins 1968). Organisms will select habitats in which their survival and reproductive success is high. Organisms that select less profitable habitats will have lower survival and contribute fewer offspring to future generations. Identifying preferred habitats by animals is therefore fundamental to the understanding of the relationship between animals and their environment. Patterns of habitat selection, however, may depend on the spatial and temporal scale at which habitat selection is examined (e.g., Orians and Wittenberger 1981; Wiens et al. 1987; Wiens 1989; Schaefer and Messier 1995).

Ecologists are now aware that study conclusions may depend on the spatial or temporal scale of observation (Allen and Starr 1982; O'Neill et al. 1986; Wiens 1989; Duarte 1991; Levin 1992; Allen and Hoeskstra 1993). Ecological variability can be viewed as structured in a nested array of scales of variation, each contributing part of

the global variability and presenting patterns that may differ from level to level (Duarte 1991). The selection of habitats by animals, too, can be viewed as a hierarchical process (Johnson 1980; Senft et al. 1987). An organism first selects a general area in which to live, and then makes subsequent decisions about the use of different patches or habitats within that area, and its responses to different food-types encountered (Johnson 1980).

Johnson (1980) identified four spatial scales of habitat selection. Adhering to the fundamentals of hierarchy theory (Allen and Starr 1982; O'Neill et al. 1986; O'Neill 1989; Allen and Hoekstra 1993), these spatial scales of habitat selection correspond to different rates of selection processes. First order selection is the selection of the physical or geographic range of a species, and may be determined over periods of evolutionary time. Second order selection determines the home range of an individual within the geographic range of the species, and is determined over the lifetime of an animal. Third order selection determines feeding sites within the home range that may be selected on a daily or hourly basis. Fourth order selection is defined by foraging decisions like prey choice or choice of browse within a feeding site. These decisions may be made on a minute-by-minute or even second-by-second basis.

Factors affecting survival and reproduction can differ from one level of habitat selection to the next (e.g., Orians and Wittenberger 1991; Schaefer and Messier 1995; Rettie and Messier 2000). Rettie and Messier (2000) suggested that selection patterns for animals should permit them to avoid the effects of those factors most able to limit individual fitness, and selection patterns that allow for this should

be strongest at the coarsest (largest) scales. Therefore, the selection of habitats at larger scales may differ from the selection of habitats at smaller scales. Failure to view habitat selection as a hierarchical process could result in a narrow and possibly misleading notion of the value of habitats to animals.

Habitat selection by grizzly bears (*Ursus arctos*) in North America has been studied for over fifty years, largely in the Rocky Mountains and Alaska (reviews in Jonkel 1987; LeFranc et al. 1987; Craighead et al. 1995). Only a minor fraction of all grizzly bear selection studies, however, have explored patterns at more than one scale of selection (e.g., MacHutchon et al. 1993). In this Chapter I examine the habitat selection patterns of a previously unstudied population of barren-ground grizzly bears inhabiting Canada's central Arctic. I assess habitat selection at two scales: Johnson's (1980) second and third orders of selection.

At the second order of selection I compare the availability of habitat types in the home ranges of study animals to the availability of habitat types in the entire study area (Roy and Dorrance 1985; Thomas and Taylor 1990). At the third order of selection I compare the proportional use of habitat types within a bear's home range to the proportional availability of habitat types within the home range. Here, buffers around individual telemetry locations are used to determine proportional use of habitat types (Rettie and McLoughlin 1999; Rettie and Messier 2000). The area available for habitat use varies from one location to the next and depends upon the amount of elapsed time between successive telemetry locations (Arthur et al. 1996). I use resource selection functions to determine relative selection of habitats by grizzly bears (Manly et al. 1993; Boyce and McDonald 1999). Formally, my null hypotheses

are that, at both orders of selection, all habitat types are used proportionately to their availability by grizzly bears.

3.2 Methods

3.2.1 Study Area

The study area was located in Canada's central Arctic, encompassing approximately 75,000 km^2 (Fig. 3.1; roughly 1/3 of the main study area due to the limited availability of habitat maps required for analysis; see Chapter 1, Fig. 1.1). The region is characterized by short, cool summers and long, cold winters. Summer temperatures average 10°C and winter temperatures are commonly below -30°C; the area is semi-arid with annual precipitation around 300 mm, about half of which falls as snow (BHP Diamonds Inc., 1995, Ecological mapping: 1995 baseline study update, Yellowknife, Northwest Territories, Canada). Drainages support willow (*Salix* spp.) and dwarf birch (*Betula glandulosa*) shrubs as tall as 3 m, and birch shrublands (<0.5 m in height) dominate the uplands. Shrubs such as blueberry (*Vaccinium uliginosum*), cranberry (*Vaccinium vitis-idaea*), and crowberry (*Empetrum nigrum*) are common and their berries are important foods to grizzly bears (Gau 1998). The Bathurst caribou (*Rangifer tarandus*) herd migrates annually through the study area. The herd leaves wintering grounds below the treeline in April, travels to calving grounds near the community of Bathurst Inlet by early June, and disperses south in late summer and autumn. The herd was estimated at 349,000 ± 95,000 caribou >1 year of age in 1996 (Gunn et al. 1997). Muskox (*Ovibos*

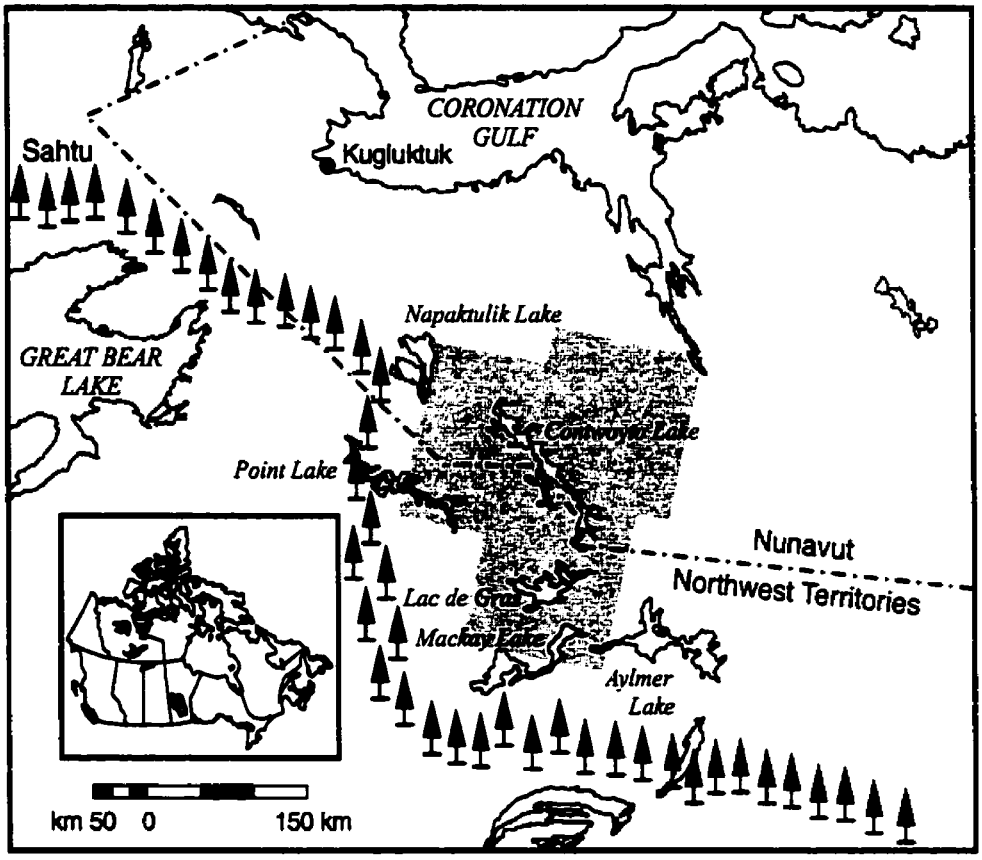

Fig. 3.1. Study area covered by classified Landsat TM images in the central Arctic and available for the analysis of grizzly bear habitat selection patterns.

moschatus) occur sporadically in the northern half of the study area. Much of the study area is part of a well-drained peneplain with lakes in the hollows and scattered depressions. Rounded rocky hills and glacio-fluvial features such as eskers, kames, drumlins, and raised beaches are often the only major relief features.

3.2.2 Animal Capture and Telemetry

Satellite radio-telemetry (Service Argos Inc., Landover, Maryland, USA) was used to obtain habitat use data from barren-ground grizzly bears. Satellite telemetry provides continued and precise (approximately ±0.5 km, SD) information on bear movements with minimum disturbance to bears (Fancy et al. 1988; Harris et al. 1990). Satellite collars (Telonics, Mesa, Arizona, USA) were equipped with a VHF beacon to permit locations of radio-marked animals from an aircraft and, eventually, for the retrieval of collars. Most collars were designed to transmit approximately two to five latitude-longitude locations every two days (eight-hour duty cycle) from 1 May–1 November. During other months, collars were programmed to transmit locations every eight days to minimize output of battery power.

Between May 1995 and June 1999, a Bell 206B or Hughes 500 helicopter was used to search for and capture bears. A Piper Supercub, Scout, or Aviat Husky aircraft equipped with skis or floats was sometimes used for more intensive searches of the study area. Most grizzly bears were captured in spring during the snow melt period (15 May–5 June) by following tracks in the snow. Field crews immobilized bears with an injection of tiletamine hydrochloride and zolazepam hydrochloride (Telazol®, Ayerst Laboratories Inc., Montreal, Quebec, Canada) from a projected

dart. Immobilized animals were marked with identification numbers applied as ear tags and permanent lip tattoos. Bears were weighed using a load-cell scale (Norac Systems International Inc., Saskatoon, Saskatchewan, Canada) while suspended in a cargo net from a helicopter. We measured heart girth, straight-line body length, skull length, and skull width with a tape measure and calipers, and extracted a vestigial premolar tooth for age determination (Craighead et al. 1970). Some bears were tested for nutritional condition using bioelectrical impedance analysis and blood sampling (Gau 1998). Only those bears weighing >110 kg (males) and >90 kg (females) were fitted with satellite radio-collars prior to release.

3.2.3 Habitat Maps

I used a combination of three Landsat Thematic Mapper (TM) scenes classified by the Northwest Territories Centre for Remote Sensing to determine the availability of habitat types to grizzly bears in the study area (Epp and Matthews 1998). Twelve discrete habitat types excluding water and ice are represented in the maps (Table 3.1), including: esker habitat, wetlands, tussock/hummock successional tundra, lichen veneer, spruce forest, boulder fields, exposed bedrock, riparian tall shrub habitat, birch seep, typical heath tundra, heath tundra with >30% boulder content, and heath tundra with >30% bedrock content (Epp and Matthews 1998). All spatial analyses described herein were conducted using SPANS® Explorer™ 7.0 (Tydac Research Inc., Nepean, Ontario, Canada).

Table 3.1. Land habitat types identified in the three Landsat TM images by the NWT Centre for Remote Sensing and used in the analysis of habitat selection by grizzly bears (adapted from Epp and Matthews 1998).

Lichen Veneer	This ecosystem unit characterizes areas covered with continuous mats of lichen that appears as a "veneer". These sites are windswept and dry, allowing for little other plant growth. Lichen veneer consists mainly of mosses (e.g., *Aulacomnium turgidum, Dicranum acutifolium, Polytrichum junipernum*, and species of *Sphagnum*), several species of *Cetraria, Alectoria, Cladina*, and *Cladonia, Thamnolia vermicularis*, and others.
Esker Complex	Esker complexes include all communities occurring on esker landforms. Esker tops are usually sparsely vegetated; common species include three-toothed saxifrage (*Saxifraga tricuspidata*) and moss-campion (*Silene acaulis*) with lesser amounts of crowberry (*Empetrum nigrum*) and bearberry (*Arctostaphylos spp.*). Lee slopes support bands of dwarf birch (*Betula glandulosa*) and willow (*Salix* spp.) that may reach heights of 1 m.
Wetland	This ecosystem unit is made up of sedge meadows (composed primarily of *Carex* and *Eriophorum* spp.), and occasionally sedge fens (common species include *Carex aquatilis, Carex rotundata, Eriophorum angustivolium*, and *Potentilla palustris*) and emergent plant communities (common species include *Arctophila fluva* and *Ranunculus pallasii*).
Tussock/Hummock	This ecosystem unit occurs on moist to sub-hygric lower slopes and depressions where tussocks (and hummocks) form. Tussocks are composed primarily of mounds of sheathed cotton-grass (*Eriophorum vaginatum*); later stage hummocks are typified by dwarf birch (*Betula glandulosa*). Labrador tea (*Ledum decumbens*), cloudberry (*Rubus chamaemorus*), and Labrador lousewort (*Pedicularis labradorica*) are also common.
Heath Tundra	This ecosystem unit delineates the typical mesic tundra habitat. Boulder and bedrock content is below 30%. Vegetation is dominated by a well-developed mat of low shrubs including dwarf birch (*Betula glandulosa*), Arctic willow (*Salix arctica*),

Continued...

	northern Labrador tea (*Ledumn decumbens*), crowberry (*Empetrum nigrum*), cranberry (*Vaccinium vitis-idaea*), black and red bearberry (*Arctostaphylos spp.*), and blueberry (*Vaccinium uligonosum*). Herb and moss layers are not well developed.
Heath Bedrock	Heath tundra in which boulder content ranges from 30–80% coverage.
Heath Boulder	Heath tundra in which exposed bedrock content ranges from 30–80% coverage.
Spruce Forest	Localized to the southern part of the study area, where the transition between boreal forest and tundra is more pronounced. Species include white spruce (*Picea glauca*), jack pine (*Pinus banksiana*), and white birch (*Betula papyrifera*). Where conditions are more favourable, spruce-lichen woodlands exits.
Tall Shrub Riparian	This ecosystem unit occurs in active stream channels on fluvial veneers of fine-textured materials overlying boulders. The productive soil medium and constant availability of flowing water supports a tall shrub community (up to 4 m in height) of dwarf birch (*Betula glandulosa*), willow (*Salix* spp.), green alder (*Alnus crispa*), and occasionally white spruce (*Picea glauca*; only in southern and southwestern portions of the study area). The herb layer is also well developed with bluejoint (*Calamagrostis canadensis*), dwarf raspberry (*Rubus arcticus*), dwarf marsh-violet (*Viola epipsila*), and horsetail (*Equisetum arvense*) as common species.
Birch seep	This ecosystem unit occurs in areas of active seepage through boulder fields. Typical vegetation is relatively well-developed dwarf birch (*Betula glandulosa*; 1 to 3 m tall) with an herb layer of bluejoint (*Calamagrostis canadensis*). Fine-textured fluvial deposits may occur in boulder crevices but rooting is primarily in the flowing water.
Bedrock Field	Exposed bedrock with a coverage in excess of 80%.
Boulder Field	Boulder fields with a coverage in excess of 80%. Boulders support a community of rock lichens of *Umbilicaria* spp., *Rizcarpon geographicum*, *Xanthoria elegans*, *Parmeliopsis ambigua*, and other species.

3.2.4 Second Order Selection

Analysis of second order selection patterns (Johnson 1980) was based on the methods of Manly et al. (1993), and considered the study area as available and each home range as the area used by study animals. I estimated home (primarily annual) ranges for grizzly bears using the fixed kernel technique with least squares cross-validating (LSCV) to determine bandwidths (Silverman 1986; Worton 1989*a*,*b*, 1995), as this was the least biased method available (Seaman and Powell 1996, Seaman et al. 1999). I chose the 95% isopleth to measure home ranges, but exclude occasional sallies. I calculated home ranges using "The Home Ranger", Version 1.1 (F.W. Hovey, British Columbia Forest Service, Research Branch, Columbia Forest District, P.O. Box 9158, R.P.O. No. 3, Revelstoke, BC V0E 3K0, Canada). Radio locations used in calculating home ranges were a minimum of 48 hours apart, and included locations only of Service Argos classes one, two, and three[•]. I included only those ranges that overlapped the mapped study area by a minimum of 60.0% for second order selection analysis.

For both habitat availability and use I divided the area of each of the 12 habitat types by the total study area or home range of an individual (less built-up areas such as mine sites and areas of water), respectively. The resulting sets of used and available habitat ratios, which always totalled 1.0, were used to calculate a

[•] Locations are categorized by Service Argos to indicate accuracy on a scale of 3, 2, 1, 0, A, B, and Z, with 3 being the highest quality location. Only classes 1, 2, and 3 are given error estimates. Reported accuracies for locations are: class 1, 68% of locations are accurate within 1000 m; class 2, 68% of locations are accurate within 350 m; class 3, 68% of locations are accurate within 150 m. Location accuracy can be influenced by the stability of a transmitter's oscillator, the elevation of the transmitter, ionospheric propagation errors, and errors in satellite orbital data.

resource selection index (Manly et al. 1993: 40-41) for each of the H habitat types, for each bear in each home range. The selection ratios for each home range were first calculated as:

$$w_i = \frac{proportion\ used_i}{proportion\ available_i}$$

and then standardized using the following equation:

$$b_i = \frac{w_i}{\sum_{i=1}^{H} w_i}$$

The resource selection function (the set of b_i's, where $i = 1$ to H and H is the number of habitat types) for an individual bear was considered to be the basic datum for subsequent statistical analyses.

3.2.5 Third Order Selection

For analysis of third order selection patterns (Johnson 1980), methods were adapted from those presented by Arthur et al. (1996), whereby the areas available for habitat use by an animal from one location to the next (as determined from satellite telemetry) depended upon the amount of elapsed time between successive locations. I determined the radii for measuring availability for each satellite location observation according to a function derived from the 95th percentile of distances moved over hourly periods by grizzly bears in this study (Fig. 3.2), bounded by the limits of the home range of an animal. I defined habitat used as the contents of a circle 2.0 km in

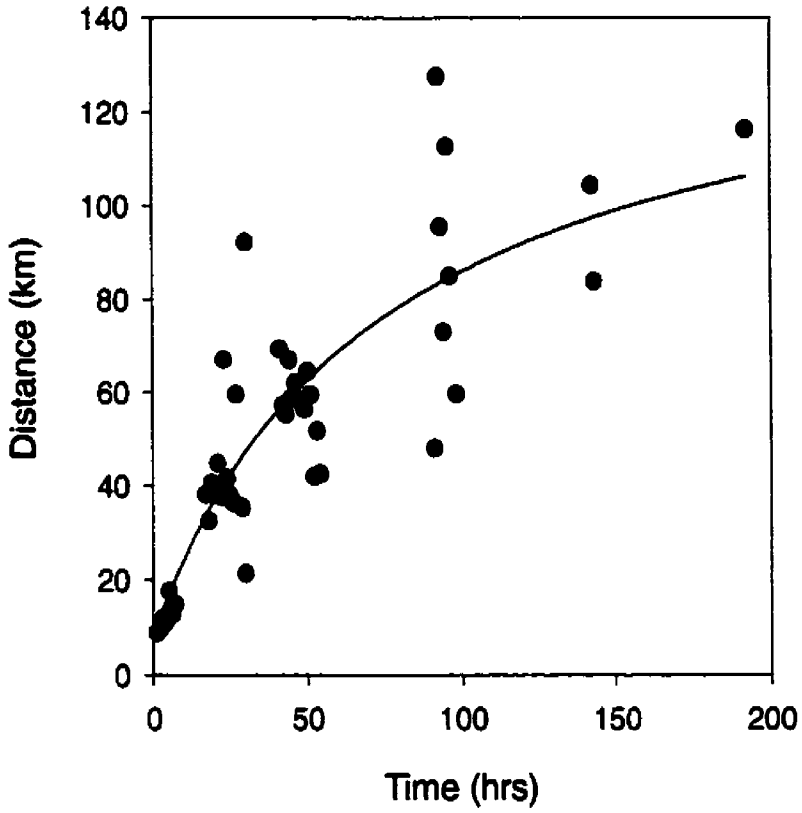

Fig. 3.2. Distance moved as a function of time for grizzly bears in the study area. Each data point represents the 95th percentile of distance moved for time intervals between successive satellite telemetry locations. The equation for the line is $y = 8.51 + 136.05*x/(75.43*x)$.

radius, centred on a telemetry location (Rettie and McLoughlin 1999; Rettie and Messier 2000). The analysis was based only on locations with tested accuracy (i.e., Service Argos classes one, two, and three).

Here, each buffer of use may be thought to conform to the general area used by a bear within a period of less than one hour. After 1.0 hour but less than 1.1 hours the average distance traversed by a bear from a previous location was 2.09 km (S.E. = 0.16, $n = 85$). Specifying a use radius of 2.0 km allowed me to employ successive satellite locations with temporal differences of as little as one hour, because after one hour grizzly bears, on average, have moved greater than two kilometres away from any given point location.

For both use and availability I divided the area of each habitat type within a buffer by the total area of the buffer. The resulting sets of used or available habitat ratios totalled 1.0 for each telemetry location. Data were processed with a program written in C^{++} to determine sets of standardized resource selection functions (i.e., the sets of H resource selection indices (b_i) where $i = 1$ to H and H is the number of habitat types) according to formulae in Arthur et al. (1996).

Four seasons were defined for analysis of third order selection patterns by referring to temporal changes in the diet of barren-ground grizzly bears (obtained from scat analyses of study animals; Gau 1998), which include: spring (den emergence–20 June); summer (21 June–31 July); late summer (1 August–9 September); and autumn (10 September–denning).

The resource selection function for each animal season was considered the basic "sampling unit" for subsequent analyses at the third order of selection. For this

level of analysis, the spruce forest habitat type (Table 3.1) was eliminated for both use and availability. Spruce forest was found only in the southern- and westernmost parts of the study area and outside the home ranges of several study animals. A habitat type must be greater than zero in availability for a resource selection index to be calculated (otherwise there is a problem of division by zero). Including spruce forest in the seasonal analysis would have prevented resource selection functions from being calculated for those bears that did not have access to spruce forest in their home ranges.

3.2.6 Statistical Analysis

For both second and third order selection analyses, all values of b_i were rank-transformed prior to statistical analysis to enable the use of parametric methods with decidedly non-parametric data (Conover and Iman 1981). Following the methods of Arthur et al. (1996) the selection indices for each bear or bear season were used to create H - 1 synthetic variables based on differences in adjacent pairs of ranked b_i values. I employed the synthetic variables to conduct multivariate analyses of variance (MANOVA) with the objective of examining the effects of sex and/or reproductive status in females, and season (third order selection only), on habitat selection patterns (SPSS Inc., Chicago, Illinois, USA). The MANOVA procedure employed is analogous to a multivariate repeated-measures ANOVA design (Johnson and Wichern 1982; SPSS Inc. 1993). For the MANOVA and subsequent post-hoc analyses at the third order of selection I decided to weigh each resource selection function (bear season) by the number of circular buffers used to determine the

resource selection function with a weighted least-squares (WLS) regression model (SPSS Inc. 1993). All post-hoc multiple comparisons were conducted using the Welsch step-up procedure (Welsch 1977; Sokal and Rohlf 1995: 252–254) on ranks of b_i-values. An experimentwise alpha value of 0.10 was used for all tests of significance.

3.3 Results

3.3.1 Second Order Selection

The 95% fixed-kernel home ranges of nine male bears, six female bears without accompanying young, and eight female bears with accompanying young were available for analyzing second order selection patterns. Multivariate analysis of variance indicated that there was no significant difference between sex or reproductive status with regard to habitat selection patterns at the second order of selection (Wilks' Lambda, Approx. $F_{22,20} = 1.41$, $P = 0.22$). That is, both males, lone females, and females with cubs were practicing the same selection patterns when establishing their home ranges in the study area. After pooling the two female samples, I again failed to detect a difference in habitat selection patterns between the sexes (Wilks' Lambda, Approx. $F_{11,11} = 1.27$, $P = 0.37$).

Mean ranks of selection index values and significant differences among habitat types as determined from multiple comparison tests on ranks of habitat selection indices (both sexes combined) are presented in Fig. 3.3. Esker habitat was preferred above all other habitats. That is, when compared to the habitats available in

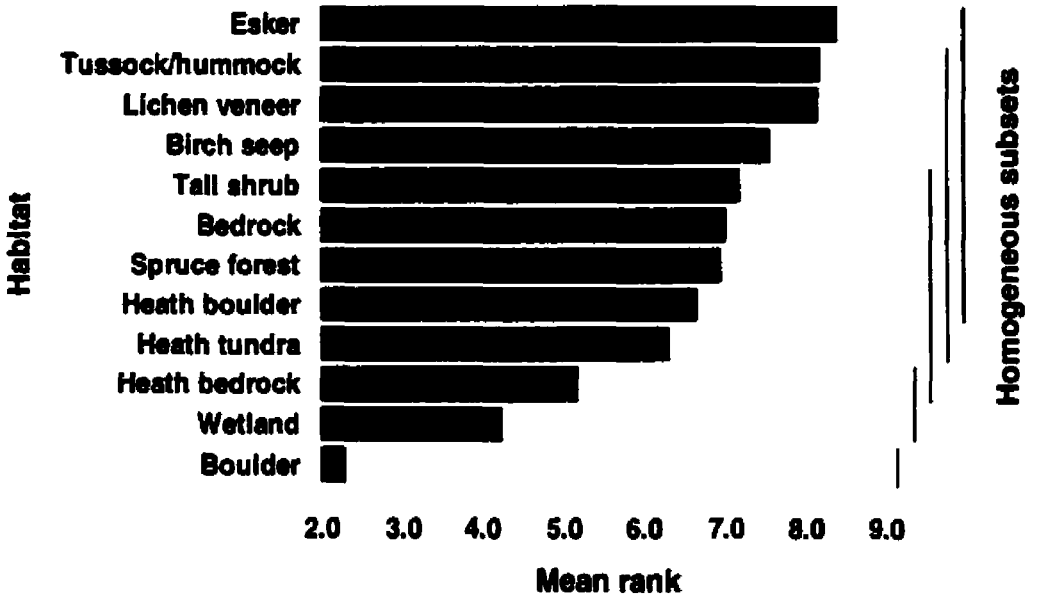

Fig. 3.3. Mean ranks of habitat selection indices (b_i) for grizzly bears ($n = 23$) at the second order of selection. Homogeneous subsets of data are indicated at right for mean ranks which are not significantly different (experimentwise $\alpha = 0.10$; Welsch's multiple range test).

the study area, the home ranges of study animals contained preferentially more esker habitat when compared to other habitats. Next, relative to other habitats, bears preferentially selected for tussock/hummock successional tundra, lichen veneer, and birch seep. Selection for these three habitat types was followed by preferential selection for tall shrub riparian areas, bedrock regions, spruce forests, heath/boulder, and heath tundra. Wetlands were significantly less preferred when compared to these habitats. Boulder fields were significantly less preferred when compared to all other habitat types, including wetlands.

3.3.2 Third Order Selection

A total of 2,833 class one, 2,435 class two, and 1,121 class three locations from 26 male and 20 female grizzly bears were available for analyzing third order selection patterns. Multivariate analysis of variance indicated significant differences in patterns of habitat selection among levels of sex/reproductive status (Wilks' Lambda, Approx. $F_{20,412} = 3.32$, $P < 0.001$) and season (Wilks' Lambda, Approx. $F_{30,605} = 2.71$, $P < 0.001$). I observed no interaction between sex/reproductive status and season (Wilks' Lambda, Approx. $F_{60,1084} = 1.04$, $P = 0.41$). Post-hoc analyses revealed that for at least one synthetic variable the mean for males significantly differed from lone females, and for at least one synthetic variable the mean for males significantly differed from females with cubs. Further, for at least one synthetic variable the mean for lone females differed significantly from females with cubs. Post-hoc analyses also revealed significant differences among means of all possible pairs of seasons for at least one synthetic variable.

For all levels of sex/reproductive status in each season I present mean ranks of selection indices and significant differences among habitat types as determined from multiple comparison tests on ranks of habitat selection indices (Figs. 3.4–3.7). In spring, grizzly bears demonstrated greatest preference relative other habitats for esker habitat, regardless of reproductive status. Notwithstanding reproductive status, bedrock and lichen veneer habitats were also generally favoured by bears over other habitat types. In addition, males showed high preference relative other habitats for the tussock/hummock successional tundra, heath tundra, and tall shrub riparian zones. Females without accompanying young also showed preference for tall shrub habitat; however, females with cubs did not.

In summer, males continued to demonstrate significant preference for tussock/hummock successional tundra, and high ranks for typical heath tundra and tall shrub riparian zones. Females with and without cubs demonstrated highest preference for tall shrub riparian habitat and eskers. Heath tundra was also preferred by females with accompanying young.

In late summer, esker and tall shrub riparian habitat again emerged as two of the most preferred habitats by bears. Although esker habitat was highly preferred by males and lone females, it was not, however, highly ranked by females with accompanying cubs. High ranks of tall shrub riparian habitat were observed for bears regardless of sex/reproductive status. Males continued to prefer tussock/hummock successional tundra, which females with accompanying young also expressed some preference.

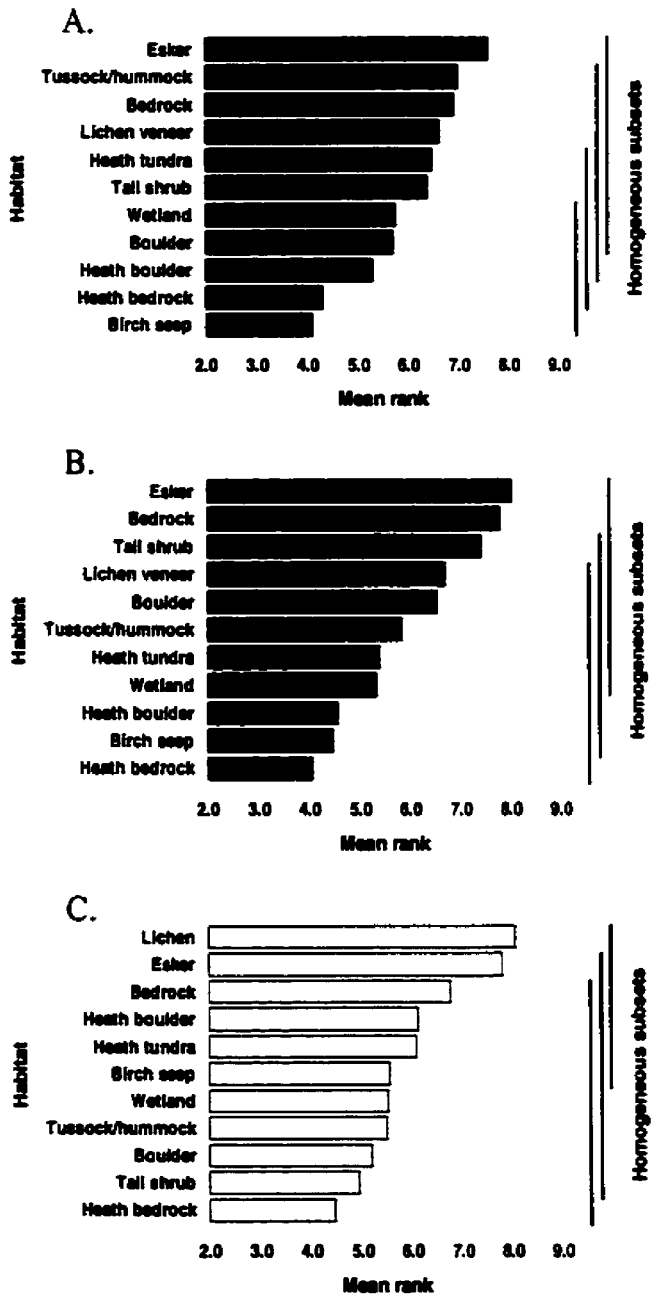

Fig. 3.4. Mean ranks of habitat selection indices (b_i) for grizzly bears at the third order of selection in spring (den emergence–20 June). A. Males ($n = 32$); B. Females without cubs ($n = 14$); C. Females with cubs ($n = 19$). Homogeneous subsets of data are indicated for mean ranks which are not significantly different (experimentwise $\alpha = 0.10$; Welsch's multiple range test).

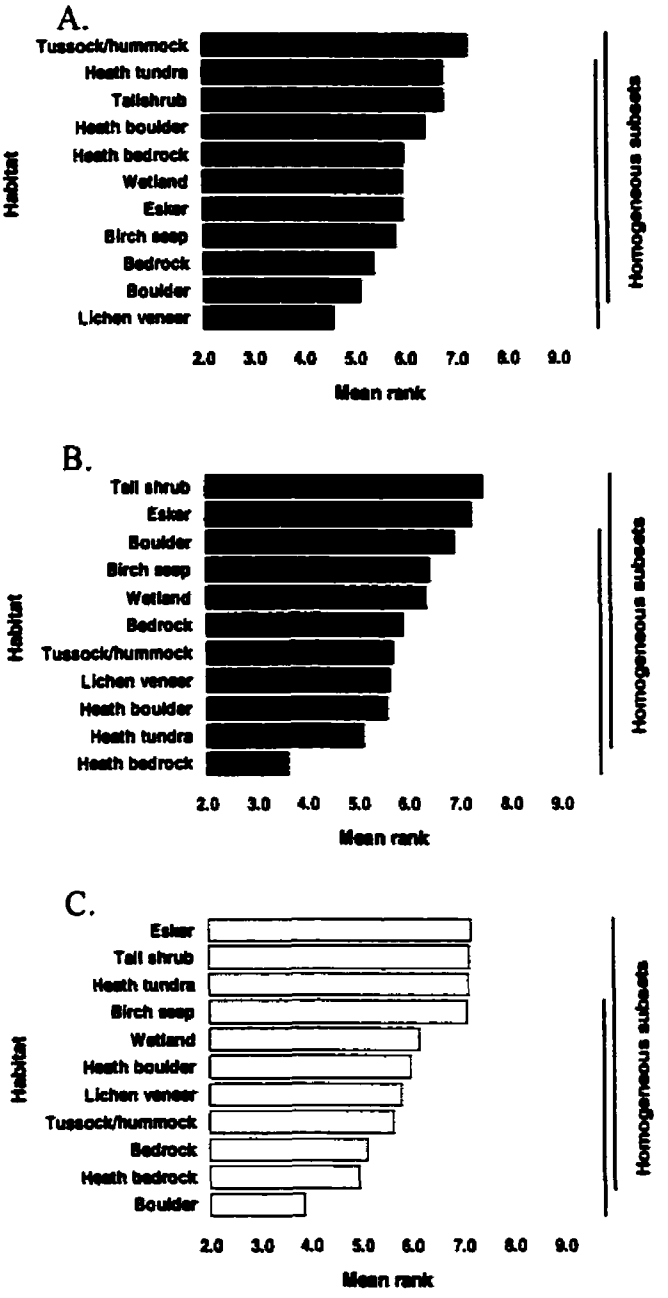

Fig. 3.5. Mean ranks of habitat selection indices (b_i) for grizzly bears at the third order of selection in summer (21 June–31 July). A. Males (n = 28); B. Females without cubs (n = 18); C. Females with cubs (n = 16). Homogeneous subsets of data are indicated for mean ranks which are not significantly different (experimentwise α = 0.10; Welsch's multiple range test).

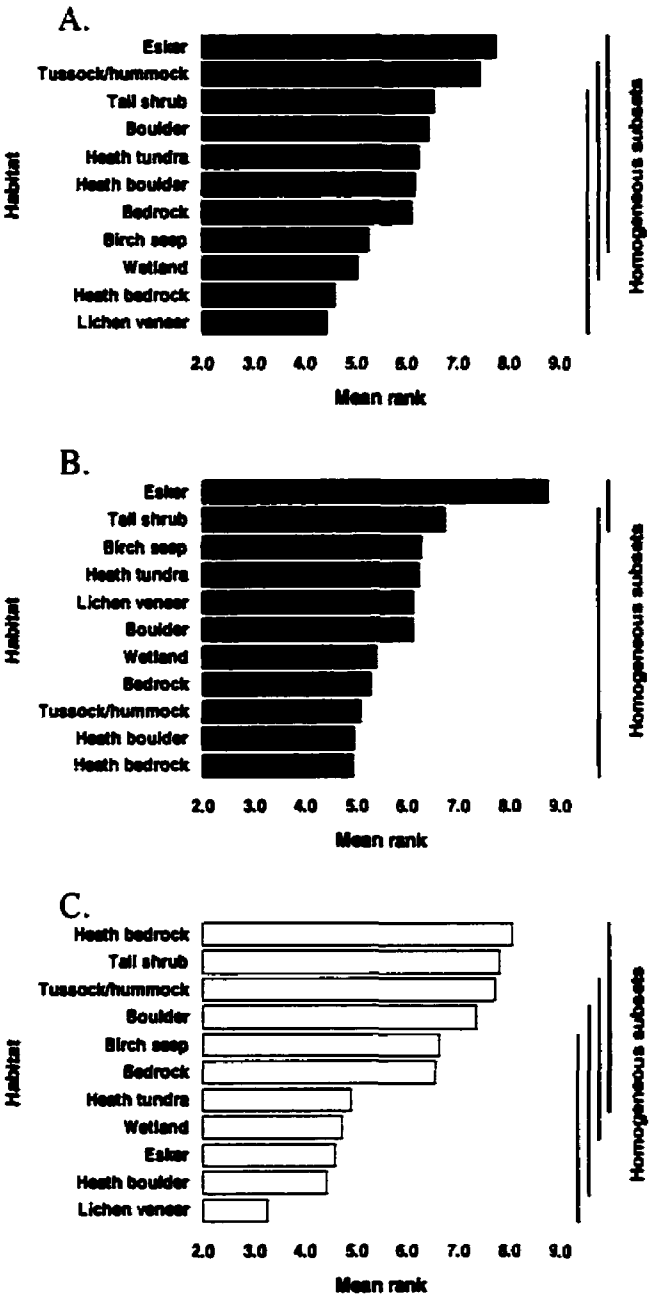

Fig. 3.6. Mean ranks of habitat selection indices (b_i) for grizzly bears at the third order of selection in late summer (1 August–9 September). A. Males ($n = 24$); B. Females without cubs ($n = 22$); C. Females with cubs ($n = 11$). Homogeneous subsets of data are indicated for mean ranks which are not significantly different (experimentwise $\alpha = 0.10$; Welsch's multiple range test).

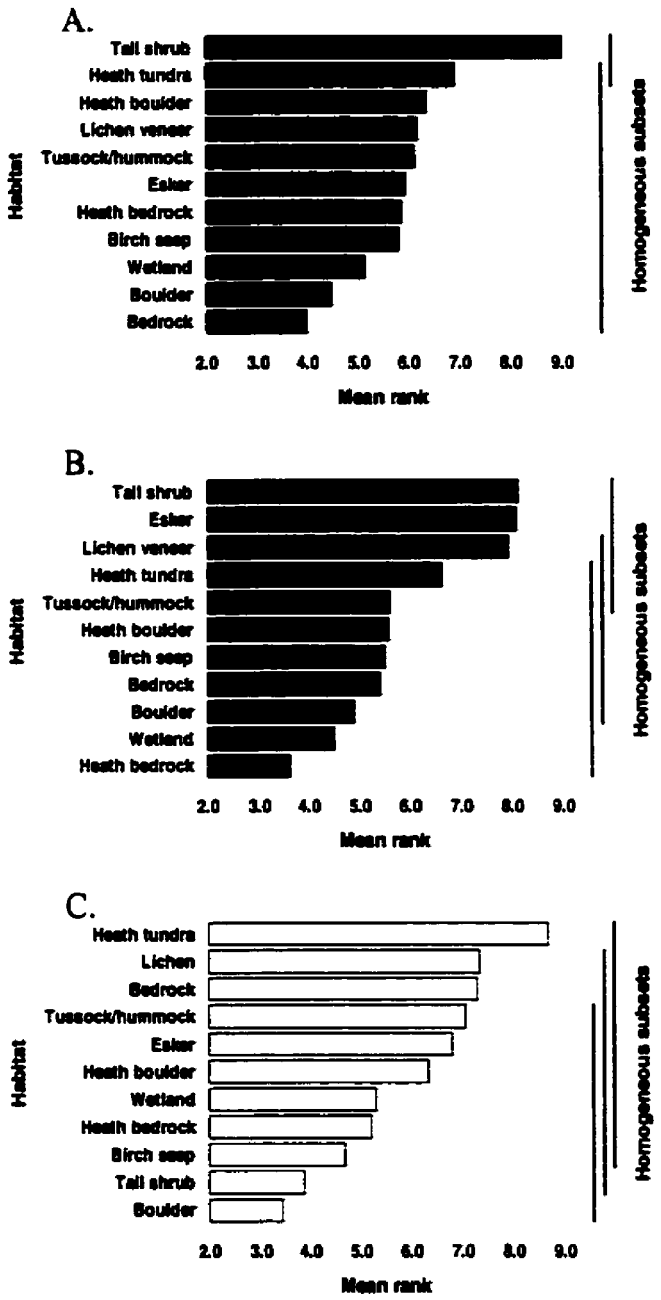

Fig. 3.7. Mean ranks of habitat selection indices (b_i) for grizzly bears at the third order of selection in autumn (10 September–den entrance). A. Males (n = 19); B. Females without cubs (n = 15); C. Females with cubs (n = 9). Homogeneous subsets of data are indicated for mean ranks which are not significantly different (experimentwise $\alpha = 0.10$; Welsch's multiple range test).

In autumn, there was a demonstrated preference by males for tall shrub riparian zones. Lone females also showed highest preference for this habitat. The preference for tall shrub riparian zones observed by male and lone female grizzly bears was not, however, shared by females with cubs. Esker habitat continued to be highly ranked by lone females. Lichen veneers were significantly preferred or at least highly ranked by bears of all levels of sex/reproductive status.

Overall, esker and riparian tall shrub habitats were the most preferred habitats by bears throughout the year. Tussock/hummock successional tundra was also favoured by males at varying times during the year. In addition, lichen veneers were favoured in spring and autumn by most bears. There was a general pattern of avoidance of the highest-ranked habitat for males by females with cubs in summer, late summer, and autumn. This pattern of habitat use was not observed for lone females.

3.4 Discussion

Rettie and Messier (2000) pointed out that selection patterns for animals should permit them to avoid the effects of those factors most able to limit individual fitness, and selection patterns that allow for this should be strongest at the coarsest (largest) scales. Less important limiting factors may influence habitat selection patterns only at smaller scales of selection. For example, woodland caribou likely select habitats at higher orders of selection to minimize wolf predation, or exposure to the lethal meningeal worm (Rettie and Messier 2000). Only at finer scales would

foraging decisions of caribou determine habitat selection patterns (Rettie and Messier 2000). The effects of a given limiting factor on habitat selection may persist, however, over a broad range of scales (i.e., a broad domain). This may be especially true if important limiting factors cannot be addressed solely by habitat selection patterns at higher orders of selection (Rettie and Messier). For example, because predation is the most important limiting factor in woodland caribou, if attempts to avoid predators at coarser scales of selection do not meet with success caribou may need to continue to select habitat to minimize predation at finer scales of selection (Rettie and Messier 2000).

Barren-ground grizzly bears in the study area are likely not limited by interspecific predation, human hunting, or disease. Therefore, I predicted that the patterns of selection observed by barren-ground grizzly bears at the coarser scale (second order selection) examined in this study would likely correspond to factors such as food abundance or food availability in time and space (i.e., grizzly bears in the central Arctic are likely food-limited). Because grizzly bears in the central Arctic inhabit one of the least productive and most seasonal regions of North America (Chapter 4; McLoughlin et al. 2000), I would not expect bears to meet nutrition demands solely at the level of the home range (i.e., second order selection). That is, bears may need to vary their focus on habitats within home ranges to meet energy demands (i.e., third order selection); each habitat likely provides different food values to bears at different times during the year. Therefore, I also predicted that patterns of selection for barren-ground grizzly bears at the finer scale of study (third order selection) would focus on vegetation communities identified at the coarser scale, but

selection for these habitats would vary throughout the year. Further, if barren-ground grizzly bears are limited by intraspecific predation, I predicted that sexual segregation in habitat use should be apparent at one or both scales of habitat selection. These predictions are supported here.

This study documents highly selective patterns of habitat selection by barren-ground grizzly bears. Selection was demonstrated at both spatial scales examined, and for different seasons at the third order of selection. The habitats selected at the second order (coarser scale) were largely selected at the third order (finer scale). The general pattern was for bears to preferentially select esker habitat, tall shrub riparian habitat, tussock/hummock successional tundra, and lichen veneers relative to other habitat types for both orders of selection examined. Some habitats, such as tall shrub riparian habitat, which was only moderately preferred at the coarser order of selection, became highly preferred at the finer order of selection. Relative preference for habitats varied according to sex or reproductive status and season at the third order of selection.

Males and females may be preferring to use eskers and exposed areas of bedrock relative to other habitat types during the spring season because these areas are likely the first to become snow-free, providing the easiest access to late-season berry crops of the previous year (primarily crowberry, *Empetrum nigrum*, and cranberry, *Vaccinium vitis-idaea*). Bears may preferentially select eskers throughout the entire year, however, because eskers provide easy and convenient travel routes. Further, eskers may provide cover for hunting or contain more abundant game than other habitats. Grizzly bears in the study area are decidedly carnivorous, more so

than bears found in the interior of North America (Gau 1998). Arctic ground squirrels (*Spermophilus parryii*), an important component of the diet of barren-ground grizzly bears in late summer and autumn (Tuktoyaktuk Peninsula, Northwest Territories, Nagy et al. 1983*a*; Western Brooks Range, Alaska, Hechtel 1985; the central Arctic, Gau 1998), may be found more easily or captured more easily in esker habitat. Soils in eskers are less compacted than those found elsewhere in the study area (e.g., glacial till), which may allow for easier excavation of ground squirrel burrows. Grizzly bears will also preferentially den in eskers (Chapter 5).

Tall shrub riparian habitat may be important to bears during summer, late summer, and autumn for several reasons. Patches of dwarf birch and willow >1 m in height may provide bears with overhead hiding cover or thermal cover. Further, tall shrub areas contain concentrations of several foods that are used by grizzly bears at varying times in the year (mainly summer and late summer), such as horsetail (*Equisetum* spp.), sedges (*Carex* spp., *Eriophorum* spp.), and willow buds (Gau 1998). Tall shrub drainage habitats that structurally resemble the tall shrub riparian zones of this study were used more than expected by grizzly bears on the tundra of the Arctic National Wildlife Refuge in Alaska (Phillips 1987) and Ivvavik National Park, Yukon (MacHutchon 1996). Phillips (1987) concluded that tall shrub zones restricted to the margins of rivers and streams were used primarily for bedding and for feeding on herbaceous plants in summer (July), and for feeding on the roots of alpine hedysarum (*Hedysarum alpinum*) in fall (August). MacHutchon (1996) determined that tall shrub drainage habitats (Willow-Coltsfoot, Alaska Willow Drainage, Willow Floodplain) were preferentially used for feeding on horsetail,

mountain sorrel (*Oxyria digyna*), and bearflower (*Boykinia richardsonii*) in summer, and for bedding throughout the year. Our study area contains little or no bearflower nor alpine hedysarum (Porsilid and Cody 1980; Gau 1998; *personal observation*). The tall shrub riparian habitats in the study area may be of different food value to bears than those found along the Arctic coastal plain of Alaska and the north slope of the Yukon. For example, grizzly bears in the central Arctic may rely on tall shrub riparian habitat more for ambush habitat while preying on caribou or muskox (see, e.g., Reynolds and Garner 1987), rather than for grazing foods.

Tussock/hummock successional tundra may provide high-quality bedding habitat to bears in summer and late summer. Grizzly bears were observed to dig beds in hummocky rises sometimes to permafrost (also observed in Ivvavik National Park, Yukon; MacHutchon 1996), perhaps to avoid overheating in summer. Further, beds in open, windy areas with low shrub cover may provide relief from biting insects in summer and late summer. Hummocky tundra and typical heath tundra may provide important concentrations of blueberry (*Vaccinium uliginosum*), bearberry (*Arctostaphylos rubra* or *alpina*), crowberry, and cranberry in late summer, and over-wintered patches of berries in spring. Earlier successional stages of tussock tundra provide concentrations of sedges (*Carex* spp.) and Arctic cotton grass (*Eriophorum vaginatum*), both of which were major constituents of summer scat volumes in study animals (Gau 1998). Hechtel (1985) reported that the floral parts of cottongrass, a good source of nitrogen and phosphorus (Kuropat and Bryant 1980), are an important spring food for barren-ground grizzly bears in northwest Alaska. Similar to this study, Phillips (1987) noted greater than expected use of tussock tundra by grizzly

bears early in the year at the Arctic National Wildlife Refuge, Alaska. Phillips (1987), however, did not observe any grazing of the floral parts of cottongrass by bears despite its relative abundance in the refuge.

Lichen veneers may attract caribou, which are specialist foragers of lichens, and offer hunting habitat for grizzly bears throughout the year. Highest use of lichen veneers occurred during spring and autumn when caribou migrate through most of the home ranges of grizzly bears in this study. Caribou were preyed on extensively by grizzly bears at these times (Gau 1998). In spring, caribou remains constituted approximately 61% of scat volumes from study animals; in late summer and autumn caribou remains represented between 62–75% of scat volumes (Gau 1998). The high preponderance of protein from caribou in the diet of grizzly bears in the study area may result from low availability of plants that are naturally rich in protein, such as alpine hedysarum. The roots of alpine hedysarum are an important source of seasonally available protein for grizzly bears in most other northern environments (e.g., Nagy et al. 1983*a*,*b*; Hechtel 1985; Phillips 1987; MacHutchon 1996). Indeed, in areas where protein-rich plant foods such as the roots of alpine hedysarum are common, protein from mammals such as caribou may comprise only a minor component of the diet of grizzly bears—even when ungulates are in relative abundance (e.g., in the presence of the Porcupine caribou herd, Arctic Mountains, Yukon, Nagy et al. 1983*b*; Ivvavik National Park, Yukon, MacHutchon 1996).

Females with accompanying young did not generally exhibit the same patterns of habitat selection throughout the summer, late summer, and autumn as males and lone females. This may be a strategy to avoid males, which have been noted to prey

on females and their cubs (e.g., Jonkel 1987; McLellan 1994). Intraspecific predation on female barren-ground grizzly bears in the central Arctic has been previously documented. In an earlier study near the community of Kugluktuk, two of 15 radio-collared female bears were apparently killed by large—likely male—bears (Case and Buckland 1998). Although no cubs were known to be killed by male grizzly bears in the study by Case and Buckland (1998), in a study of barren-ground grizzly bears on the Tuktoyaktuk Peninsula, Northwest Territories, Nagy et al. (1983*a*) recorded three instances where adult males were suspected of killing cubs. A further study of grizzly bears on the north slope of Alaska documented male predation of females and their cubs (Reynolds 1980). During this study a yearling cub disappeared during a period in which the cub and its mother were observed to be followed by an adult male grizzly bear. The mother was observed to mate with the accompanying male shortly after her cub disappeared. This observation suggests infanticide, a well-documented behaviour in grizzly bears (McLellan 1994), on the part of the accompanying male. The apparent segregation between males and females with cubs with respect to habitat use may be a strategy to avoid intraspecific predation or infanticide.

Sexual segregation in habitat selection, as a possible strategy by females with cubs to minimize contact with aggressive males, has also been suggested for grizzly bears in northwest Alaska (Ballard et al. 1993) and Alberta (Wielgus and Bunnell 1995*a*,*b*). In these cases females were displaced by larger males from areas of perceived higher habitat quality to areas of lower habitat quality. Displacement of females with cubs by males to poorer quality habitat is also suggested by the results of this study. The habitats from which females with cubs were apparently

displaced—primarily esker and tall shrub riparian zones—appear to offer bears access to valuable food and cover resources (Gau 1998). Similar to this study, females with cubs-of-the-year used tall shrub riparian habitats less than males and females in the Arctic tundra of northwest Alaska (Ballard et al. 1993).

It is also interesting that the apparent segregation in habitat use between females with cubs and males, to some degree, infers segregation in habitat use between females with cubs and lone females (males and lone females showed greater similarity in habitat selection patterns). It may be that females with cubs are avoiding lone females in addition to males; however, intrasexual predation and infanticide is rare among female grizzly bears (for review see McLellan 1994). A more likely explanation is that females with cubs are less able to defend themselves and their families, or escape from, aggressive males than are lone females. Greater ease in avoidance of aggressive males by lone females may permit access to habitats in which males are more likely to be encountered. Of course, in spring and summer lone females share preferred habitats with males to secure matings. Sharing preferred habitats with males for mating does not, however, account for differences in habitat selection patterns between lone females and females with cubs in late summer and autumn. The latest record of paired mates in this study occurred at the end of July, which coincides with the end of the mating season observed in most other grizzly bear populations (LeFranc et al. 1987).

No differences in the habitat selection patterns between males, lone females, and females with accompanying young were found to occur at the coarser level (second order) of selection. This is important. That sexual segregation in habitat

selection appears to be scale dependent concurs with the results of Bower and Kie (1996), and for grizzly bears, the results of Wielgus and Bunnell (1995*a*,*b*) and Mace and Waller (1997). As in this study, Mace and Waller (1997) concluded that at the home range level of selection female avoidance of males did not occur. Although Mace and Waller did not examine male/female interactions at finer levels of selection, the results of Wielgus and Bunnell (1995*a*,*b*) agree with my results by suggesting that differences in habitat selection between sexes does indeed occur at smaller spatial scales. Whereas food availability may be the limiting factor affecting habitat selection patterns at the higher level of selection; intraspecific predation, in concert with food availability, may be influencing habitat selection at the lower level of selection.

Patterns of habitat selection at larger scales may differ from patterns of habitat selection at smaller scales (Johnson 1980; Orians and Wittenberger 1981; Senft et al. 1987; Wiens et al. 1987; Wiens 1989; Schaefer and Messier 1995). The results of this study suggest that at higher scales, food availability may be the most important limiting factor for grizzly bears: patterns of habitat selection appeared to emphasize foraging habitats. This pattern was also generally demonstrated at the finer level of selection; however, unlike at the second order of selection, at the third order of selection sexual segregation in habitat use was also evident. This suggests that intraspecific predation also may be affecting habitat selection at the third order of selection. The notion that intraspecific predation may affect habitat selection patterns at the finer, but not the coarser, level of selection, may indicate that it is less able to limit population size than those factors governing higher order selection patterns

(Rettie and Messier 2000). Selection patterns for animals should permit them to avoid the effects of those factors most able to limit individual fitness, and selection patterns that allow for this should be strongest at the coarsest (largest) scales (Rettie and Messier 2000). Results of this study underline the importance of scale dependence in habitat selection. Failure to view habitat selection as a hierarchical process may result in a narrow and possibly misleading notion of habitat selection patterns.

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4. EFFECT OF TEMPORAL AND SPATIAL DIFFERENCES IN HABITAT ON HOME RANGES OF BARREN-GROUND GRIZZLY BEARS IN THE CENTRAL ARCTIC

4.1 Introduction

Animal movements show discontinuities over time and space, and one way of describing spatial limitations of movement involves the concept of home range. The home range of an animal is generally defined as the area typically used, over some specified period of time (e.g., breeding season, year, lifetime), to carry out the activities of securing food, mating, and caring for young (Burt 1943). Thus, a home range describes the relationship between an individual's movements and time (Fig. 4.1).

The central problem of what determines home range size is the immensely integrative nature of the home range. Several ecological and physiological factors are thought to influence home range size (review in McLoughlin and Ferguson 2000). McNab (1963) was first to demonstrate that home range size is positively associated with body size in mammals, and suggested that home range size may be related to an animal's size-dependent metabolic rate. Other factors that may affect home range size include social organization (Damuth 1981), population density (e.g., Desy et al. 1990; Wolff 1985, 1993; Wolff and Schauber 1996), and risk of predation (e.g., Desy

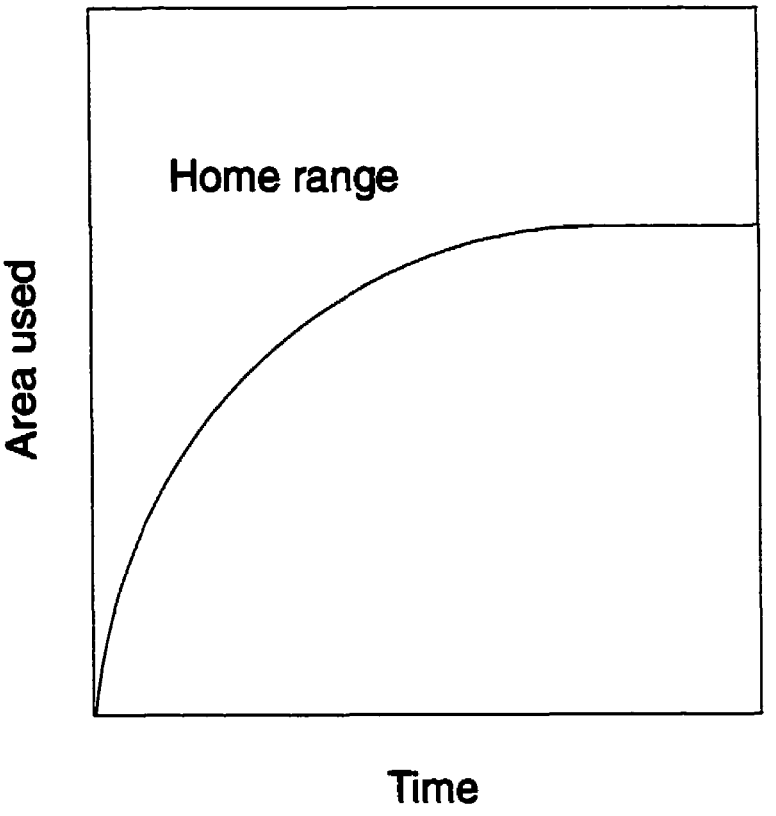

Fig. 4.1. Animal movements will describe a home range if new areas are less likely to be used with greater time (i.e., an asymptotic value is approached).

et al. 1990; Tufto et al. 1996). Further, because survival and reproduction are often food-limited, the abundance and predictability of food in time and space are also considered to be important factors influencing home range size (McLoughlin and Ferguson 2000). The abundance and predictability of food in the environment is one measure of the quality of a habitat for an animal. Thus, temporal and spatial variation in habitat likely affect home range size.

In this Chapter, I describe the home ranges of grizzly bears in Canada's central Arctic (Chapter 1; Fig. 1.1). I assess the importance of habitat as a determinant of home range size at two levels: 1) the individual level, which compares the size of home ranges across individuals within a single population; and, 2) the population level, which compares the average home range size among populations within the same species (McLoughlin and Ferguson 2000). I examine the effects of both temporal and spatial variation in habitat on home range size for grizzly bears in the central Arctic. To understand temporal fluctuations in movement patterns, I describe changes in the seasonal ranges of grizzly bears in the central Arctic. To assess the effect of spatial differences in habitat on home range size I explore relationships between proportional availabilities of habitat types within the home ranges of grizzly bears in the central Arctic and range size. I hypothesize that if bears are responding to the availability of different habitats in the environment, home ranges should vary with the proportional availability of habitat types within the home range. For example, home ranges may increase as the proportion of habitats in the home range that provide poor food value to bears increases, or as quality habitats become more patchily distributed within a matrix of poor quality habitats. At the level of the

population, I further examine the effects of spatial differences in habitat on home range size. Here, I test a possible explanation for why the mean annual ranges of barren-ground grizzly bear populations are generally larger than interior and Pacific-coastal populations of grizzly bears. I hypothesize that bears have responded to low primary productivity in Arctic tundra environments with large ranges to obtain requisite food resources.

4.2 Methods

4.2.1 Study Area

The study area was located in Canada's central Arctic, encompassing approximately 235,000 km^2 of mainland Nunavut and the Northwest Territories (Chapter 1, Fig. 1.1). The study area was delineated, clockwise, by the community of Kugluktuk, the Kent Peninsula, Aylmer Lake, Mackay Lake, and Great Bear Lake. The region is characterized by short, cool summers and long, cold winters. Summer temperatures average 10°C and winter temperatures are commonly below -30°C; the area is semi-arid with annual precipitation around 300 mm, about half of which falls as snow (BHP Diamonds Inc., 1995, Ecological mapping: 1995 baseline study update, Yellowknife, Northwest Territories, Canada). Drainages support willow (*Salix* spp.) and dwarf birch (*Betula glandulosa*) shrubs as tall as 3 m, and birch shrublands (<0.5 m in height) dominate the uplands. Shrubs such as blueberry (*Vaccinium uliginosum*), cranberry (*Vaccinium vitis-idaea*), and crowberry (*Empetrum nigrum*) are common and their berries are important foods to grizzly bears

(Gau 1998). The Bathurst caribou (*Rangifer tarandus*) herd migrates annually through the study area. The herd leaves wintering grounds below the treeline in April, travels to calving grounds near Bathurst Inlet by early June, and disperses south in late summer and autumn. The herd was estimated at 349,000 ± 95,000 caribou >1 year of age in 1996 (Gunn et al. 1997). Muskox (*Ovibos moschatus*) occur sporadically in the northern half of the study area. Much of the study area is part of a well-drained peneplain with lakes in the hollows and scattered depressions. Rounded rocky hills and glacio-fluvial features such as eskers, kames, drumlins, and raised beaches are often the only major relief features.

4.2.2 Animal Capture and Telemetry

Satellite radio-telemetry (Service Argos Inc., Landover, Maryland, USA) was used to obtain movement data on barren-ground grizzly bears. Satellite telemetry provides continued and precise (approximately ±0.5 km, SD) information on bear movements with minimum disturbance to bears (Fancy et al. 1988; Harris et al. 1990). Satellite collars (Telonics, Mesa, Arizona, USA) were equipped with a VHF beacon to permit locations of radio-marked animals from an aircraft and, eventually, for the retrieval of collars. Most collars were designed to transmit approximately two to five latitude-longitude locations every two days (eight-hour duty cycle) from 1 May–1 November. During other months, collars were programmed to transmit locations every eight days to minimize output of battery power.

Between May 1995 and June 1999, a Bell 206B or Hughes 500 helicopter was used to search for and capture bears. A Piper Supercub, Scout, or Aviat Husky

aircraft equipped with skis or floats was sometimes used for more intensive searches of the study area. Most grizzly bears were captured in spring during the snow melt period (15 May–5 June) by following tracks in the snow. Field crews immobilized bears with an injection of tiletamine hydrochloride and zolazepam hydrochloride (Telazol®, Ayerst Laboratories Inc., Montreal, Quebec, Canada) from a projected dart. Immobilized animals were marked with identification numbers applied as ear tags and permanent lip tattoos. Bears were weighed using a load-cell scale (Norac Systems International Inc., Saskatoon, Saskatchewan, Canada) while suspended in a cargo net from a helicopter. We measured heart girth, straight-line body length, skull length, and skull width with a tape measure and calipers, and extracted a vestigial premolar tooth for age determination (Craighead et al. 1970). Some bears were tested for nutritional condition using bioelectrical impedance analysis and blood sampling (Gau 1998). Only those bears weighing >110 kg (males) and >90 kg (females) were fitted with satellite radio-collars prior to release.

4.2.3 Annual Ranges

From satellite telemetry locations I estimated annual ranges for grizzly bears using the fixed kernel technique with least squares cross-validating (LSCV) to determine bandwidths (Silverman 1986; Worton 1989*a*,*b*, 1995), as this was the least biased method available (Seaman and Powell 1996, Seaman et al. 1999). I chose the 95% isopleth to measure annual ranges, but exclude occasional sallies. I calculated annual ranges using "The Home Ranger", Version 1.1 (F.W. Hovey, British Columbia Forest Service, Research Branch, Columbia Forest District, P.O. Box 9158,

R.P.O. No. 3, Revelstoke, BC V0E 3K0, Canada). Radio locations used in all analyses were a minimum of 48 hours apart. Most satellite collars in the study were designed to last for two years; hence, for some animals I obtained two annual range estimates. With these cases, to avoid sample pseudo-replication, I chose only a single annual range for inclusion in analyses (the estimate with the most locations), unless the animal underwent a change in family status between the two years (i.e., cases where females gained or lost cubs, or cubs aged). I included only those annual ranges comprised of ≥38 locations for analysis, as kernel techniques tend to overestimate range size with smaller sample sizes (Seaman et al. 1999). Also, ranges were not calculated for subadult males (2–5 years of age). Subadult male grizzly bears may wander extensively in search for a home region, and during this period they are not considered to possess a home range (Burt 1943).

4.2.4 Seasonal Ranges

Seasonal ranges were calculated only for those animals which transmitted ≥8 locations per season in every season of the year. I defined seasons according to changes in the diet of barren-ground grizzly bears during the active period (adapted from Gau 1998), including: spring (den emergence–20 June), summer (21 June–31 July), late-summer (1 August–9 September), and autumn (10 September–den entrance). Den emergence generally occurs in the last week of April and den entrance in the last week of October (Chapter 5). Because sample sizes for seasonal ranges were generally <38, I used the 95% minimum convex polygon (MCP) method to estimate seasonal ranges (Tracker, Version 1.1, Camponotus AB, Solna, Sweden).

When the number of fixes is low, the MCP is more robust than other techniques (Harris et al. 1990).

4.2.5 Range and Movement Statistics

Ranges were $\log_{10}$-transformed prior to analyses to meet assumptions of normality and equal variance among groups of data (Sokal and Rohlf 1995). The annual ranges of adult males and females of differing family status were compared using a one-way analysis of variance (ANOVA). Estimates of seasonal ranges for grizzly bears across a single year were related through time; hence, to compare seasonal ranges among males and females of differing family status and among seasons, a two-way repeated-measures analysis of variance (RM ANOVA) was performed (SigmaStat, Version 2.0, Jandel Corporation, San Rafael, California, USA). Following significant ANOVAs, Tukey's HSD test (Zar 1984) was used to compare individual means.

4.2.6 Temporal and Spatial Effects of Habitat on Home Ranges of Barren-Ground Grizzly Bears

To assess the effect of temporal differences in habitat on range size, I examined changes in seasonal ranges of barren-ground grizzly bears. I then qualitatively compared these changes to changes in seasonal food availability in the study area. These results are presented in the *Discussion* (Section 4.4).

To assess the effect of spatial differences in habitat on range size, I first determined the proportion of habitats contained within the home ranges of grizzly bears. I then identified linear relationships between home range size and proportional habitat availability within home ranges. Here, home ranges were primarily annual ranges; however, to avoid pseudo-replication of data, where more than one annual range was calculated for a bear (Section 4.2.3) a composite range based on data from more than one year was used for analysis.*

The availability of habitats to grizzly bears were assessed from three Landsat Thematic Mapper (TM) scenes classified by the Northwest Territories Centre for Remote Sensing in a 75,000 km^2 portion of the study area (Epp and Matthews 1998)(Chapter 3; Fig. 3.1). Twelve discrete habitat types excluding water and ice were represented in the classified Landsat TM scenes (Chapter 3; Table 3.1), including: esker habitat, wetlands, tussock/hummock successional tundra, lichen veneer, spruce forest, boulder fields, exposed bedrock, riparian tall shrub habitat, birch seep, typical heath tundra, heath tundra with >30% boulder content, and heath tundra with >30% bedrock content (Epp and Matthews 1998). I included only those ranges that overlapped the mapped portion of the study area by a minimum of 60.0% for analysis. To determine proportional habitat availability within each range, I "stamped" the perimeter vectors of each home range (or portions thereof) on the habitat map and calculated the area of each habitat type contained within the home range vectors. I then divided the area of each of the 12 habitat types by the total

* Annual ranges of grizzly bears in this study did not differ significantly from multi-year composite ranges for both females (Paired t-test, $t_{34} = 1.79$, $P = 0.08$) and males (Paired t-test, $t_{25} = 1.70$, $P = 0.10$). If more than one annual range was calculated for a bear, the smallest annual range was used for matched comparison with the multi-year range.

terrestrial area of the range contained within the habitat map. Because habitat selection analysis indicated no differences in the proportional availability of habitat types within the home ranges of males and females of differing family status (Chapter 3), I pooled observations across sex and reproductive status for this analysis. Stepwise multiple regression (SPSS Inc. 1993; Sokal and Rohlf 1995: 610–664) was used to identify relationships between range size and proportional habitat availabilities within home ranges. All spatial analyses were conducted using SPANS® Explorer™ 7.0 (Tydac Research Inc., Nepean, Ontario, Canada).

4.2.7 Spatial Effect of Habitat on Home Ranges Among Populations of Grizzly Bears

I used site-specific measures of habitat quality to help explain observed differences between the size of grizzly bear annual ranges in the central Arctic and the reported annual ranges of several other North American grizzly bear populations. Habitat quality was estimated as net annual above ground primary productivity, which can be predicted through calculating actual evapotranspiration (Rosenzweig 1968) and using the following equation from Leith (1976):

$$PP = 3000[1-e^{-0.0009695(E-20)}]$$

where PP is primary productivity (g/m^2), E is actual evapotranspiration (mm), and e is the base of natural logarithms. For each study area in my comparison I computed values of E using the Thornthwaite method (Thornthwaite and Mather 1957; Willmot

et al. 1985). To determine whether the regression of mean annual ranges of grizzly bears against primary productivity was significant and to explore any differences between males and females, I used an analysis of covariance (ANCOVA). Because most studies of grizzly bears used the minimum convex polygon (MCP) technique to calculate annual ranges, I provided mean 95% MCP annual ranges for bears in the central Arctic for comparison purposes (1995–1997 data only; as in McLoughlin et al. 1999). Primary productivity estimates and mean male and female ranges were $\log_{10}$-transformed prior to analysis to ensure normality of data.

4.3 Results

4.3.1 Annual Ranges

I calculated 71 annual ranges from collared bears, including: 26 adult males, 22 lone females, and 23 females with cubs. Mean annual ranges significantly differed across sex and family status ($F_{2,68} = 14.2$, $P < 0.001$). The annual ranges of males ($\overline{X} = 7{,}245$ km^2, SE = 1,158) were significantly larger than lone females (Tukey's HSD, $p = 3$, $q = 6.75$, $P < 0.001$) and females with cubs (Tukey's HSD, $p = 3$, $q = 6.08$, $P < 0.001$); however, the annual ranges of lone females ($\overline{X} = 1{,}955$ km^2, SE = 349) and females with accompanying young ($\overline{X} = 2{,}239$ km^2, SE = 437) did not differ (Tukey's HSD, $p = 3$, $q = 0.72$, $P = 0.87$). I pooled females across family status and tested again for a sex effect. The mean annual range of males was larger ($F_{1,69} = 28.4$, $P < 0.001$) than the mean annual range of females pooled across family status ($\overline{X} = 2{,}100$ km^2, SE = 279).

4.3.2 Seasonal Ranges

Seasonal ranges for a complete bear-year (i.e., spring, summer, late summer, and autumn) were obtained from 16 adult males, 14 lone females, and 9 females with cubs. The size of seasonal ranges differed across sex and family status ($F_{2,108} = 19.1$, $P < 0.001$), but post-hoc analysis indicated that data for females without cubs and females with cubs should be pooled (Tukey's HSD, $p = 3$, $q = 1.08$, $P = 0.73$). A second RM ANOVA in which data from females of differing family status were pooled indicated a sex effect ($F_{1,111} = 38.1$, $P < 0.001$), a season effect ($F_{3,111} = 5.22$, $P = 0.002$), and no interaction between factors sex and season ($F_{3,111} = 0.54$, $P = 0.66$). Male seasonal ranges were consistently greater than female seasonal ranges (Fig. 4.2). Mean seasonal ranges for bears significantly decreased (Tukey's HSD, $p = 4$, $q = 5.57$, $P < 0.001$) from largest sizes in summer to smaller sizes in autumn (Fig. 4.2).

4.3.3 Spatial Effect of Habitat on Home Ranges of Barren-Ground Grizzly Bears

Stepwise multiple regression of home range size *versus* proportional habitat availability suggested a significant regression model including the predictor variables (habitats): bedrock, heath boulder, wetlands, heath bedrock, tall shrub riparian, lichen veneer, and spruce forest ($F_{7,15} = 2.25$, $R = 0.72$, $P < 0.10$). Partial regression coefficients (b) and their standard errors (SE of b), standardized partial regression coefficients (β), t-scores, P-values, and partial correlation coefficients (r_{Yi}) for each predictor variable can be found in Table 4.1. Home ranges increased with the proportion of bedrock (Fig. 4.3A) and wetlands (Fig. 4.3B) in the home range, and to

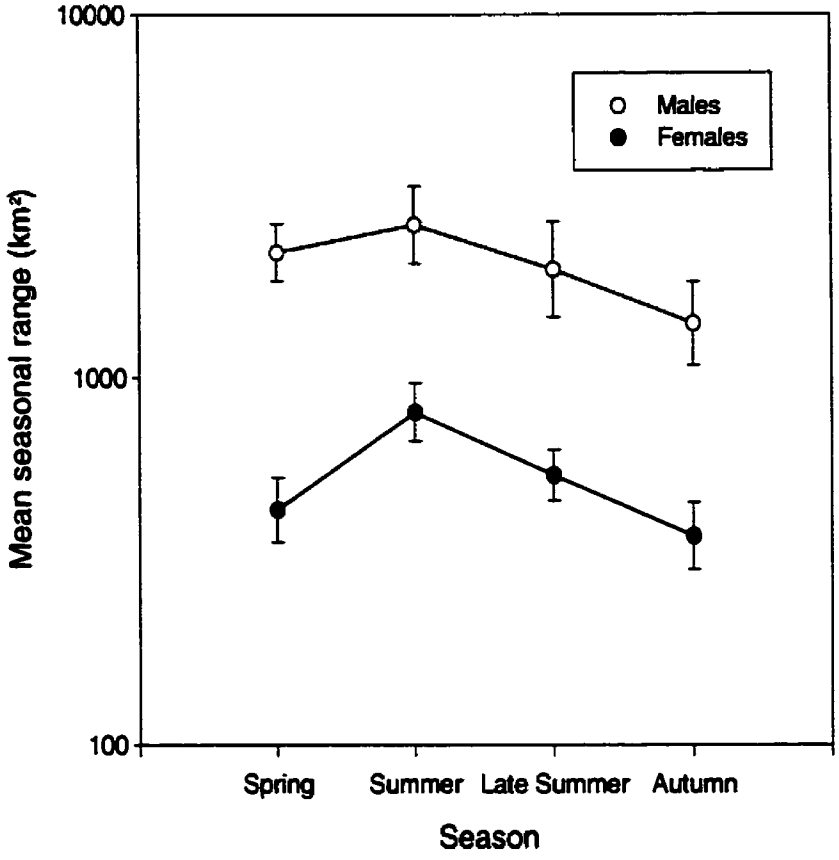

Fig. 4.2. Seasonal MCP ranges of grizzly bears in the central Arctic, 1995–1999. Means are based on data log-transformed to the base 10. Error bars are ±1 SE.

Table 4.1. Table of coefficients for significant predictor variables in the multiple regression of home range size *versus* proportional habitat availability within the home ranges of grizzly bears in the central Arctic, 1995–1999.

	Coefficients					
	b	SE	β	*t*	*P*	r_{yi}
(Constant)	-17579.3	7714.3		-2.279	0.038	
Lichen veneer	-1495.7	536.7	-0.986	-2.787	0.014	-0.58
Wetland	2154.8	751.4	1.100	2.868	0.012	0.60
Spruce forest	-16393.6	5005.7	-2.163	-3.275	0.005	-0.65
Bedrock	4368.3	1381.5	1.220	3.162	0.006	0.63
Tall shrub	7268.4	3406.6	1.245	2.134	0.050	0.48
Heath boulder	650.8	237.7	0.779	2.738	0.015	0.58
Heath bedrock	-857.9	322.6	-1.009	-2.659	0.018	-0.57

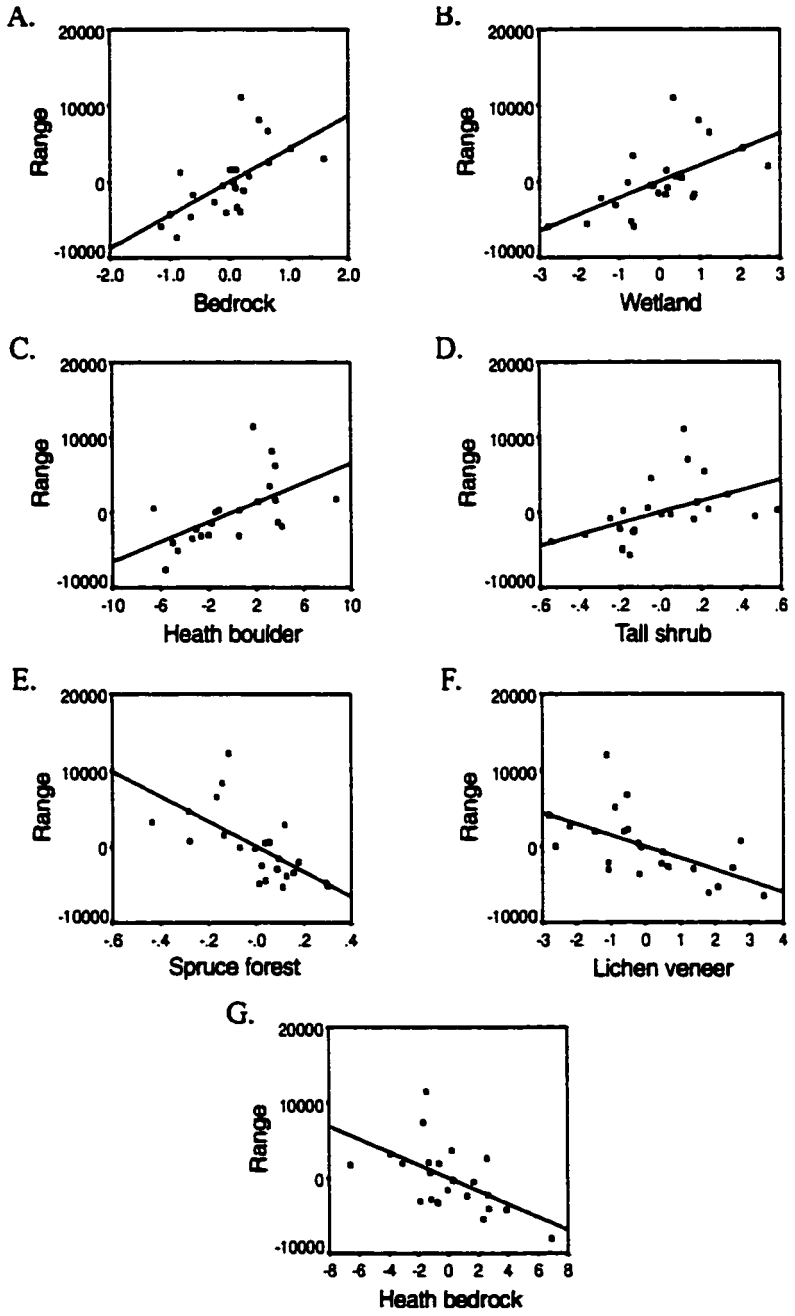

Fig. 4.3. Standardized partial regression plots of home range size *versus* predictor habitat variables for grizzly bears in the central Arctic, 1995–1999. Graphs are home range size *versus* proportional amounts of habitat within the home range: A. Bedrock; B. Wetlands; C. Heath boulder; D. Tall shrub riparian; E. Spruce forest; F. Lichen veneer; G. Heath bedrock.

a lesser extent with increasing proportions of heath boulder (Fig. 4.3C) and tall shrub riparian habitats (Fig. 4.3D). Home ranges decreased as the proportional availability of those habitats more closely associated with treeline (i.e., the southwest portion of the study area) increased within the home range. The availability of spruce forest (Fig. 4.3E) and lichen veneer habitats (Fig. 4.3F) within the home range showed strong inverse relationships with home range size. Home range size also decreased with increasing proportions of heath bedrock in the home range (Fig. 4.3G).

4.3.4 Spatial Effect of Habitat on Home Ranges Among Populations of Grizzly Bears

The mean 95% MCP annual range for adult males in this study (1995–1997 data only, McLoughlin et al. 1999) was 8,171 km^2 (SE = 1,309, n = 19); for females it was 2,434 km^2 (SE = 647, n = 35). Both means were larger than the mean annual ranges calculated using the 95% fixed kernel technique with LSCV; however, results of a paired t-test (1995–1997 data only, McLoughlin et al. 1999) indicated no difference ($t_{53} = 0.18$, $P = 0.86$) between the estimates produced by the two methods.

A survey of the published and unpublished literature revealed 27 study areas in North America for which estimates of grizzly bear annual ranges have been reported (Table 4.2). I found a significant negative relationship between documented North American grizzly bear range sizes and primary productivity for respective study areas ($F_{1,49} = 19.0$, $P < 0.001$; Fig. 4.4). Male bears, in general, possessed larger ranges than female bears ($F_{1,49} = 20.5$, $P < 0.001$; Fig. 4.4). Slopes of regression lines for males and females did not differ ($F_{1,48} = 0.04$, $P = 0.85$).

Table 4.2. Estimated mean home ranges of grizzly bears in North America. Ranges are primarily adult annual home ranges and were calculated using the minimum convex polygon (MCP) approach unless otherwise indicated. Weighted means were calculated if ranges were estimated with few numbers of locations (if data permitted). Presented in McLoughlin et al. (1999) and reprinted with permission from the International Bear Association.

Study Area	Source	Males		Females	
		km^2	*n*	km^2	*n*
Admiralty Island (Hawk Inlet), Alaska	Schoen et al. (1986)	115	6	24	12
Akamina-Kishinena/Flathead, B.C.	McLellan (1981)	446	5	200	5
Alaska Peninsula	Glenn and Miller (1980)	262	4	293	30
Alaska Range	Reynolds and Hetchel (1983)	710	6	132	11
Anderson-Horton Rivers, N.W.T.	Clarkson and Liepins (1989)	3433	7	1182	14
Central Northwest Territories	This study	8171	19	2434	35
Copper River Delta, Alaska	Campbell (1985)[a]	295	2	174	4
East Front Montana	Schallenberger and Jonkel (1980)	747	5	226	3
Eastern Brooks Range, Alaska	Reynolds (1976)[b,c]	702	5	230	8
Ivvavik National Park, Yukon	MacHutchon (1996)[d]	447	8	149	15
Jasper National Park, Alberta	Russell et al. (1979)[d]	948	6	331	6
Kananaskis, Alberta	Wielgus (1986)	1198	4	179	5
Khutzeymateen River Valley, B.C.	MacHutchon et al. (1993)[d]	130	4	52	13
Kluane National Park, Yukon	Pearson (1975)	287	5	86	8
Kodiak Island, Alaska	Barnes (1990)	185	6	71	33
Mackenzie Mountains, N.W.T.	Miller et al. (1982)			265	6
Mission Mountains, Montana	Servheen and Lee (1979)	1398	3	133	2
Noatak River, Alaska	Ballard et al. (1993)	1437	15	993	33
Northern Yukon	Nagy et al. (1983*b*)[e]	645	6	210	8
Revelstoke, B.C.	Woods et al. (1997)[c]	318	23	89	14
Selkirk Mountains, Idaho	Almack (1985)			402	2
South Fork Flathead, Montana	Mace and Jonkel (1979,1980)	286	5	99	2
Tuktoyaktuk Peninsula, N.W.T.	Nagy et al. (1983*a*)[e]	1154	7	670	
Upper Susitna River Basin, Alaska	Ballard et al. (1982)[c]	769	10	408	13
West-Central Alberta	Nagy et al. (1988)[e]	1918	17	364	
Western Brooks Range, Alaska	Reynolds (1980)	872	14	225	35
Yellowstone National Park, Wyoming	Blanchard and Knight (1991)	874	28	281	48

[a]Cited in LeFranc et al. (1987:28-30).
[b]Ranges calculated using the modified exclusive boundary technique.
[c]Estimate contains some multiannual ranges.
[d]Weighted means calculated from data presented.
[e]Weighted means cited in Nagy and Haroldson (1990). For females, data is presented as the midpoint between the mean for females with and without young except for the Northern Yukon, where the mean is only for females without young.

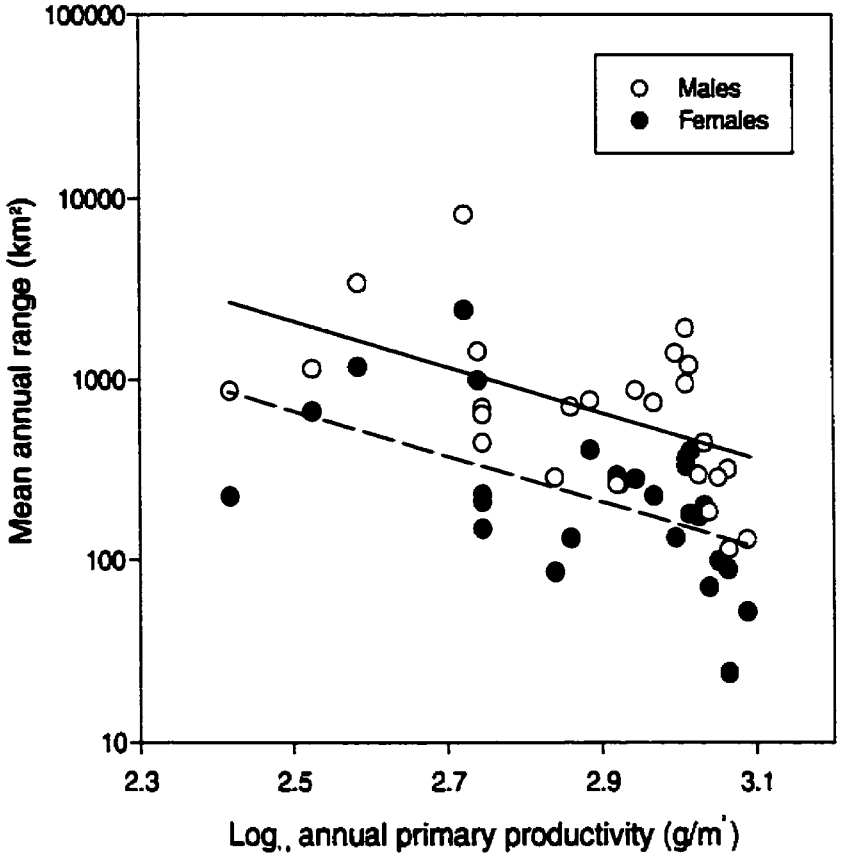

Fig. 4.4. Mean annual ranges (km^2) of grizzly bears for selected North American populations *versus* $\log_{10}$ mean annual primary productivity (g/m^2). The equation for the male regression line (solid line) is $y = 1620000 - 17.4x$. The equation for the female regression line (dashed line) is $y = 1170000 - 17.4x$. R^2 for the ANCOVA was 0.45. Presented in McLoughlin et al. (1999) and reprinted with permission from the International Bear Association.

4.4 Discussion

The annual and seasonal ranges of barren-ground grizzly bears in the central Arctic were always greater for males than for females. Gau (1998) determined that male grizzly bears in the central Arctic have higher daily energy requirements than females. Generally, a larger energy demand will necessitate a larger area for food gathering unless food is superabundant (McNab 1963). Male grizzly bears also tend to wander more in search of mates, which may further increase male ranges compared to female ranges.

I failed to detect differences among females of differing family status with regard to annual and seasonal ranges. Few studies have compared home ranges among female grizzly bears of differing family status. Pearson (1975) indicated that female ranges in southern Yukon contracted when females were accompanied by cubs of the year, but expanded when young reached yearling status, although this was not tested statistically. A trend of increasing range size as cubs age or are lost has also been observed among female grizzly bears by Blanchard and Knight (1991) in Yellowstone National Park, Nagy et al. (1983*a*) on the Tuktoyaktuk Peninsula, Northwest Territories, and MacHutchon (1996) in Ivvavik National Park, northern Yukon. Non-significant differences in ranges of females with cubs and females without cubs have been obtained from brown bears in southcentral Alaska (Ballard et al. 1982), on Kodiak Island (summer ranges compared only, Barnes 1990), and in the Khutzeymateen valley of British Columbia (MacHutchon et al. 1993). Real differences among ranges of female grizzly bears of differing family status likely do

exist, but the differences may be only of short duration (e.g., occurring only during the first few seasons after cubs of the year leave dens, or during years with two- or three-year old cubs), and hence difficult to test with the sample sizes of most telemetry studies.

The results of this study suggest that within the study population (i.e., at the level of the individual, McLoughlin and Ferguson 2000), home range size is influenced by temporal changes in the abundance and distribution of food. Here, observed seasonal trends in ranges for barren-ground grizzly bears in the central Arctic likely reflect seasonal changes in food availability. The large ranges exhibited by both sexes in summer probably result from low summer food availability, which may predispose bears to wander more in search of food. Fat stores reach annual lows in the summer, when female caribou aggregate on calving grounds beyond the ranges of most study animals and prior to the ripening of berries (Gau 1998). The subsequent decrease in range size by both sexes as the summer progresses likely reflects increased food availability. By late summer, the migratory Bathurst caribou herd returns to the central study area (where the majority of bears in this study were collared) and berries peak in abundance. Range size may lessen when food supply increases over time, and vice versa. For example, an inverse relationship between range size and annual hard mast (acorns, hickory nuts, hazel nuts) production was documented for female black bears in North Carolina (Powell et al. 1997). Following the closure of garbage dumps in Yellowstone National Park (1968–1970), the mean annual ranges of male and female grizzly bears increased five-fold before apparently levelling off in the mid-1980's (Craighead et al. 1995). Within a population, other

factors that may affect range size over time include temporal changes in behaviour, such as mate-searching behaviour. For example, male barren-ground grizzly bears travel at their highest rates during spring and summer, when they are searching for mates (McLoughlin et al. 1999). Higher rates of movement may translate into larger ranges.

In addition to temporal changes in habitat, spatial differences in habitat likely influence the size of grizzly bear home ranges within the central Arctic. Multiple regression revealed that home ranges of barren-ground grizzly bears increased with increasing proportions of bedrock, wetland, and heath boulder habitats within home ranges. Habitat selection analysis indicated that throughout most of the year these habitats are not highly ranked by bears (Chapter 3). Food in these habitats may be limited, or only accessed by bears during very short junctures in the year (e.g., bedrock during the snow-melt period as it may be one of the first habitat types to become snow-free; Chapter 3). Here, home ranges likely increase in size as the proportional amount of energetically "useless" space in the environment increases in order to supply constant amounts of quality habitat, such as esker, tall shrub riparian habitat, and tussock/hummock successional tundra (Chapter 3). Although tall shrub riparian areas—a highly ranked habitat by bears (Chapter 3)—also showed a positive relationship with home range size, the partial correlation with home range size was the weakest of all habitats included in the regression model ($r^2 = 0.23$). Further, the decision to include tall shrub riparian habitat in the regression was based on only a marginally significant ($P = 0.05$) improvement in the model.

The proportions of spruce forest and lichen veneer in home ranges—two habitats that are closely associated with the treeline of the southwest portion of the study area—showed strong negative relationships with home range size. This is interesting in that it suggests that bears that are closer to treeline require smaller home ranges to meet food demands. Bears closer to treeline may access more abundant or different foods than those bears in areas of open tundra, such as the highly favoured roots of alpine hedysarum (*Hedysarum alpinum*) that are unavailable in the central study area (Porsilid and Cody 1980; Gau 1998; *personal observation*). The roots of alpine hedysarum are an important source of seasonally available protein for grizzly bears in most other northern environments (e.g., Nagy et al. 1983*a*,*b*; Hechtel 1985; Phillips 1987; MacHutchon 1996). Within populations, home range size generally shares an inverse relationship with food abundance (McLoughlin and Ferguson 2000). This is true for several species, including voles, *Microtus townsendii* (Taitt 1981); bandicoots, *Isoodon obesulus* (Broughton and Dickman 1991); roe deer, *Capreolus capreolus* (Tufto et al. 1996); black bears, *Ursus americanus* (Powell et al. 1997); lizards, *Scleroporus jarrovi* (Simon 1975); and birds (Hixon 1980).

Apart from habitat-specific food availability, other factors governing home range size within populations may include conspecific density and risk of predation (McLoughlin and Ferguson 2000). For example, low densities may reduce competition for space and allow animals to use resources over larger ranges than at higher densities. Rogers (1977) observed that female black bears extended their home ranges into areas left vacant when neighbouring females were killed. Conversely, increased intruder pressure by conspecifics may decrease home range

size (Wolff and Schauber, 1996). If the density of grizzly bears near treeline is higher than in open tundra, the observation of smaller ranges in treed habitats *versus* open habitats may proximately result from density, rather than food, effects. Ultimately, however, observed differences in home range size may be determined by habitat quality as habitat quality influences density (at least in food-limited populations). It is difficult to separate the effects of density from habitat quality on home range size as the two factors are correlated (McLoughlin and Ferguson 2000).

Predation may influence home range size via mortality of individuals (i.e., changes in density) or by initiating predator-avoidance behaviours. Intraspecific predation on female barren-ground grizzly bears in the central Arctic has been previously documented. In an earlier study near the community of Kugluktuk, two of 15 radio-collared female bears were apparently killed by large—likely male—bears (Case and Buckland 1998). Smaller home ranges of females relative males may be a response to reduce contact with males. Experimentally, prairie voles (*Microtus ochrogaster*) responded to increased predation by behaviourally reducing home range size (Desy et al. 1990).

The home ranges of barren-ground grizzly bears in the central Arctic are the largest ranges yet reported for grizzly bears in North America. Results of my population level review show a significant inverse relationship between grizzly bear range size and primary productivity. This leads me to conclude that as within populations, habitat quality is likely an important determinant of grizzly bear home range size among populations (i.e., at the population level, McLoughlin and Ferguson 2000); hence the large annual ranges of barren-ground grizzly bear populations

relative to other populations. Variation about regression lines, however, suggests that factors other than habitat quality also may be of importance in determining range sizes of grizzly bears at the population level.

Although some variation in the data on population range sizes no doubt resulted from differences in annual range estimation techniques and sample sizes among studies, there are several other possible contributors. For example, Nagy and Haroldson (1990) concluded that differences in the size of annual ranges among four populations of grizzly bears were due largely to differences in population density. Low densities resulting from substantial human-caused mortality or other factors could feasibly reduce competition for space and allow bears to use resources over larger ranges than at higher densities. In addition, the use of ecocenters (Craighead et al. 1995) by some grizzly bear populations may contribute to smaller ranges than what would be expected from primary productivity alone. Ranges also may be inflated beyond those predicted by primary productivity if bears travel with migrating food sources such as caribou. We suspect that several bears in this study tracked the spring migration of caribou, a behaviour that has been documented in barren-ground grizzly bears in northern Alaska (Reynolds and Garner 1987). Differences in landscape topography (e.g., mountain terrain *versus* open tundra) may further affect range sizes at the population level (McLoughlin and Ferguson 2000).

The relatively large spatial requirements of grizzly bears in the central Arctic agree with results of other studies of barren-ground grizzly bears (e.g., Reynolds 1980; Nagy et al. 1983*a*; Clarkson and Liepins 1989; Ballard et al. 1993), although ranges in this study are much larger than any previously reported range estimates for

grizzly bears. Large ranges may put individual bears in contact with humans even when sites of human activity (e.g., exploration and hunting camps, industrial developments, and communities) are of considerable distance from the core of the home range of an animal. Furthermore, individual ranges of barren-ground grizzly bears could encompass several camps that are tens or even hundreds of kilometres apart. Barren-ground grizzly bears, especially those of the central Arctic, may therefore be highly susceptible to human activity. Management of bears in the central Arctic should focus on maintaining low levels of human-caused mortality, with the realization that communities, hunting camps, and mining/exploration camps may impact bears from more than just the general vicinity. Estimates of bear population status and trends should be monitored in the region to ensure that the cumulative effects of human activity on bears, including mortality, are within sustainable limits.

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5. DENNING ECOLOGY OF BARREN-GROUND GRIZZLY BEARS IN THE CENTRAL ARCTIC

5.1 Introduction

Although most grizzly bear (*Ursus arctos*) populations in North America have undergone some degree of decline or range reduction subsequent the arrival of Europeans, populations of barren-ground grizzly bears inhabiting Arctic regions of North America have remained relatively undisturbed by European settlement. Far removed from human habitation, barren-ground grizzly bears have not been subjected to the exploitation and habitat changes that led to the extirpation of grizzly bears from much of their former range. Nonetheless, all populations of grizzly bears in Canada— including barren-ground populations—are classified as "vulnerable" and considered susceptible to population decline (Committee on the Status Of Endangered Wildlife in Canada, 1991, List of species at risk, Canadian Wildlife Service, Ottawa, Ontario, Canada).

Barren-ground grizzly bears in Canada's central Arctic (Chapter 1; Fig. 1.1) may be at particular risk to population decline for several reasons, including: (1) they have limited continuity with other grizzly bear populations because they are near the northern and easternmost limit of the species' North American range, (2) because of reduced cover, bears in tundra habitats are more likely to be displaced by nearby

human activity than bears in forested areas (McLellan 1990), (3) populations of grizzly bears in tundra habitat exist at the lowest recorded densities of all extant North American grizzly bears (review in McLellan 1994), and (4) they likely have very large spatial requirements (see, e.g., Reynolds 1980; Nagy et al. 1983; Clarkson and Liepins 1989; Ballard et al. 1993), which would put individual bears in contact with humans even when developments are at considerable distance from the core of the home range of an animal.

Adding to concerns of barren-ground grizzly bear conservation in Canada's central Arctic, recent discoveries of diamonds, gold, and base metals in the region have been targeted for large-scale mining operations. Plans to develop the region include the construction of all-weather roads and infrastructures requiring granular materials from eskers, kames, and drumlins. Composed mainly of sand and gravel, eskers and related surface expressions are prominent topographic features that trace the path of collapsed depositional landforms (e.g., glacial rivers) due to melting of supporting ice (Soil Classification Working Group 1998). Previous studies in the central Arctic (Mueller 1995; Banci and Moore 1997) suggested that esker habitat was extremely important to grizzly bears, wolves (*Canis lupus*), Arctic ground squirrels (*Spermophilus parryi*), and foxes (*Vulpes vulpes* and *Alopex lagopus*) for denning. The use of granular materials by industry may therefore present a problem for the conservation of wildlife reliant upon glacio-fluvial habitats for denning, including barren-ground grizzly bears.

In order to mitigate possible conflicts between industry and the conservation of grizzly bears in the central Arctic, the extent to which bears rely on eskers and

related features for denning needs to be established. Unfortunately, preliminary studies of the denning habits of grizzly bears in the central Arctic (e.g., Mueller 1995; Banci and Moore 1997) have not been able to clearly answer this question, partly due to biases in methods of data collection. For example, both Mueller (1995) and Banci and Moore (1997) relied upon aerial and ground surveys of dens of unknown bears to collect data on denning habits, but biased their studies by spending most of their time surveying esker habitat for bear dens. Esker habitat, however, represents only ~1.5% of the landscape in the central Arctic. Further, bear dens are much easier to identify from the ground or air if excavated in open esker habitat compared to more heavily-vegetated habitats, such as tall shrub riparian areas. It is not surprising that both Mueller (1995) and Banci and Moore (1997) claimed that eskers were extremely important for grizzly bear denning relative to other habitats. These claims, however, must be interpreted with caution, and a re-evaluation of the importance of eskers as denning habitat is required before conservation recommendations to preserve esker habitat for grizzly bear denning can be effectively argued.

In this chapter, I re-evaluate the importance of eskers and other habitats as denning habitat for barren-ground grizzly bears in the central Arctic. I document the denning habits of grizzly bears in the central Arctic by following satellite and VHF radio-collared bears to their dens. By using telemetry to collect data on denning habits, I eliminate some of the biases associated with aerial and ground surveys of dens of unknown bears. I quantify the importance of esker habitat and other habitats for denning by bears, and document characteristics of recently excavated dens. Further, telemetry data allowed me to examine when grizzly bears entered and exited

dens. Data on denning chronology has not previously been reported for grizzly bears in the central Arctic.

5.2 Methods

5.2.1 Study Area

The study area was located in Canada's central Arctic, encompassing approximately 235,000 km^2 of mainland Nunavut and the Northwest Territories (Chapter 1, Fig. 1.1). The study area was delineated, clockwise, by the community of Kugluktuk, the Kent Peninsula, Aylmer Lake, Mackay Lake, and Great Bear Lake. The region is characterized by short, cool summers and long, cold winters. Summer temperatures average 10°C and winter temperatures are commonly below -30°C. The area is semi-arid with annual precipitation around 300 mm, about half of which falls as snow (BHP Diamonds Inc., 1995, Ecological mapping: 1995 baseline study update, Yellowknife, Northwest Territories, Canada). Drainages support willow (*Salix* spp.) and dwarf birch (*Betula glandulosa*) shrubs as tall as 3 m, and birch shrublands (<0.5 m in height) dominate the uplands. Shrubs such as blueberry (*Vaccinium uliginosum*), cranberry (*Vaccinium vitis-idaea*), and crowberry (*Empetrum nigrum*) are common and their berries are important foods to grizzly bears (Gau 1998). The Bathurst caribou (*Rangifer tarandus*) herd migrates annually through the study area. The herd leaves wintering grounds below the treeline in April, travels to calving grounds near Bathurst Inlet by early June, and disperses south in late summer and autumn. The herd was estimated at 349,000 ± 95,000

caribou >1 year of age in 1996 (Gunn et al. 1997). Muskox (*Ovibos moschatus*) occur sporadically in the northern half of the study area. Much of the study area is part of a well-drained peneplain with lakes in the hollows and scattered depressions. Rounded rocky hills and glacio-fluvial features such as eskers, kames, drumlins, and raised beaches are often the only major relief features.

5.2.2 Animal Capture and Telemetry

Satellite radio-telemetry (Service Argos Inc., Landover, Maryland, USA) and conventional VHF radio-telemetry were used to obtain denning information on barren-ground grizzly bears. Satellite telemetry provides continued and precise (approximately ±0.5 km, SD) information on bear movements with minimum disturbance to bears (Fancy et al. 1988; Harris et al. 1990). Satellite collars (Telonics, Mesa, Arizona, USA) were equipped with a VHF beacon to permit locations of radio-marked animals from an aircraft and, eventually, for the retrieval of collars. Most collars were designed to transmit approximately two to five latitude-longitude locations every two days (eight-hour duty cycle) from 1 May–1 November. During other months, collars were programmed to transmit locations every eight days to minimize output of battery power.

Between May 1995 and June 1999, a Bell 206B or Hughes 500 helicopter was used to search for and capture bears. A Piper Supercub, Scout, or Aviat Husky aircraft equipped with skis or floats was sometimes used for more intensive searches of the study area. Most grizzly bears were captured in spring during the snow melt period (15 May–5 June) by following tracks in the snow. Field crews immobilized

bears with an injection of tiletamine hydrochloride and zolazepam hydrochloride (Telazol®, Ayerst Laboratories Inc., Montreal, Quebec, Canada) from a projected dart. Immobilized animals were marked with identification numbers applied as ear tags and permanent lip tattoos. Bears were weighed using a load-cell scale (Norac Systems International Inc., Saskatoon, Saskatchewan, Canada) while suspended in a cargo net from a helicopter. We measured heart girth, straight-line body length, skull length, and skull width with a tape measure and calipers, and extracted a vestigial premolar tooth for age determination (Craighead et al. 1970). Some bears were tested for nutritional condition using bioelectrical impedance analysis and blood sampling (Gau 1998). Only those bears weighing >110 kg (males) and >90 kg (females) were fitted with satellite radio-collars prior to release.

5.2.3 Denning Chronology

I determined dates of den entry and den emergence for study animals from the dates on which radio-transmissions to receiving satellites ceased to be received in autumn (for den entry estimates) and the dates on which satellites resumed receiving transmissions in spring (den emergence estimates). Collar transmissions to receiving satellites were entirely blocked while bears were in their earth dens.

5.2.4 Den Characteristics

I used satellite telemetry in concert with conventional VHF telemetry to locate grizzly bear dens. Satellite radio-transmissions prior to den entrance in autumn

allowed me to determine the general location of most bear dens (i.e., within approximately 5 km). Then, using aerial telemetry later in winter (October or March), I determined the exact location of dens using a Global Positioning System (GPS). I returned to these locations the following summer (July) to investigate den characteristics.

I measured dimensions of dens where possible (i.e., entrance width and height, cavity width, height and length). I recorded the aspect of den entrances using a compass with an adjusted declination of 35° east, which is the average declination from true north for the study area. Aspect of den entrances were coded into one of four categories: north (315°–45°), east (45°–135°), south (135°–225°), and west (225°–315°). A clinometer was used to measure the slope (°) of the immediate area in which dens were excavated. I recorded the presence/absence and percentage cover of plant species (Porsilid and Cody 1980) in the immediate surroundings of den entrances (1 m radius), and estimated percent soil composition of denning habitat from close examination of den excavation soil piles (i.e., % boulder, % cobble, % gravel, % sand, % silt, % clay, % organic).

5.2.5 Denning Habitat

I recorded the general type of habitat in which dens were excavated for comparison with the availability of habitats in the study area. The availability of habitats to grizzly bears were assessed from three Landsat Thematic Mapper (TM) scenes classified by the Northwest Territories Centre for Remote Sensing in a representative 75,000 km^2 portion of the study area (Epp and Matthews 1998)(see

Chapter 3; Fig. 3.1). Twelve discrete habitat types excluding water and ice were represented in the classified Landsat TM scenes (Chapter 3; Table 3.1), including: esker habitat, wetlands, tussock/hummock successional tundra, lichen veneer, spruce forest, boulder fields, exposed bedrock, riparian tall shrub habitat, birch seep, typical heath tundra, heath tundra with >30% boulder content, and heath tundra with >30% bedrock content (Epp and Matthews 1998).

5.2.6 Statistical Analyses

Prior to statistical analyses, dates of den entrance and emergence were converted to Julian dates (days since 1 January for a given year) for use in calculations. Mean dates of den emergence and den entrance were compared across years and sexes using two-way analyses of variance (ANOVA; SigmaStat, Version 2.01, Jandel Corporation, San Rafael, California, USA). A preliminary ANOVA was conducted to determine if dates of den emergence were similar for females of differing family status (i.e., lone females *versus* females with cubs; females with cubs-of-the-year *versus* females with yearlings and two-year-olds). Following significant ANOVAs, Tukey's HSD test (Zar 1984) was used to compare individual means. Mean duration of denning (days) was calculated for those bears in which both a date of den entrance and a date of den emergence were available for any given winter. Mean duration of denning was compared between the sexes using a *t*-test.

I calculated means and standard errors of the mean (SE) for all den dimensions, estimates of den aspect, slope, percent vegetation coverage around den entrances (excluding excavation piles and caved-in portions of dens), and percentage

soil particle-size in excavation piles. Frequencies of aspect of den entrances were compared to what was expected from random using a chi-square goodness of fit test (Zar 1984; Sokal and Rohlf 1995).

The use of habitats for denning was compared to the proportional availability of habitats in the study area using a log-likelihood ratio goodness of fit test (Zar 1984: 52–53). Only those habitats in which dens were located were included for analyses, as zero values in frequency of use cannot be used in a log-likelihood ratio test. Thus, the null hypothesis tested was one of no preference for those habitats in which dens were found to occur. For habitats in which dens were not known to occur, avoidance of those habitats for denning was assumed. Following rejection of the null hypothesis, 90% Bonferroni confidence intervals were constructed for the proportion of times animals denned in each available habitat type (Neu et al. 1974). Comparison of overlap of confidence intervals to habitat availabilities was used to determine which habitat types were being preferred and/or avoided for denning (Neu et al. 1974; Byers et al. 1984; White and Garrot 1990).

5.3 Results

5.3.1 Animal Capture and Telemetry

From May 1995 to June 1999, 152 barren-ground grizzly bears were immobilized by capture crews on 264 occasions. Of these 152 individuals, 39 were adult females and 36 were adult males. Among subadults (aged three to four years), 12 were females and 10 were males. We marked 30 cubs-of-the year (16 female, 14

male), 16 yearling cubs (eight females, eight males), and nine two-year-old cubs (three females, six males). We placed 89 satellite radio-collars on 81 bears ($n = 38$ adult females, $n = 4$ subadult females, $n = 35$ males, $n = 4$ subadult males). For 23 bears (mostly females), break-away VHF radio-collars were fitted after satellite collars were removed to obtain further denning information.

5.3.2 Denning Chronology

A preliminary two-way ANOVA revealed no difference in the mean dates of den emergence for females with cubs-of-the-year, yearlings, and cubs aged two years or older ($F_{2,15} = 1.77$, $P > 0.20$). Further, dates of den emergence for these females were similar across years of study ($F_{3,15} = 1.60$, $P > 0.20$). The mean date of emergence of females with cubs (age pooled) were subsequently compared to the mean date of den emergence of females without cubs, including subadults. No difference was detected between the dates of den emergence for females with *versus* without accompanying young ($F_{1,32} = 0.34$, $P > 0.50$), although year was a significant factor in the model ($F_{3,32} = 2.73$, $P = 0.06$). Females emerged from dens significantly earlier in 1997 ($\overline{X}$ = 27 April, SE = 2.7 days, $n = 12$) when compared to 1996 ($\overline{X}$ = 8 May, SE = 2.8 days, $n = 13$) (Tukey's HSD test, $p = 4$, $q = 3.95$, $P = 0.04$). Dates of den emergence for females with and without cubs were independent of year of study ($F_{3,32} = 0.37$, $P > 0.70$).

Females pooled across family status emerged, on average, significantly later from dens than did males ($F_{1,60} = 3.11$, $P < 0.10$). Mean date of den emergence for females was 3 May (SE = 1.9 days, $n = 41$) *versus* 27 April (SE = 2.4 days, $n = 27$)

for males. Means include data from subadults ($n = 3$ estimates for females, $n = 3$ estimates for males). Mean dates of den emergence for all bears pooled across sex differed among years ($F_{3,60} = 3.26$, $P = 0.03$). As within females, both male and female bears emerged from dens significantly earlier in 1997 ($\overline{X}$ = 26 April, SE = 2.6 days, $n = 21$) when compared to 1996 ($\overline{X}$ = 7 May, SE = 2.7 days, $n = 20$; Tukey's HSD test, $p = 4$, $q = 3.86$, $P = 0.04$). There was no interaction between year and sex ($F_{3,60} = 0.09$, $P > 0.90$): females and males adjusted their den emergence patterns similarly between years 1996 and 1997.

No effect of year was detected in the comparison of female and male (including subadult) dates of den entry for years 1995–1998 ($F_{3,71} = 0.50$, $P > 0.60$). However, females entered dens ($\overline{X}$ = 16 October, SE = 1.5 days, $n = 40$) significantly earlier ($F_{1,71} = 15.2$, $P < 0.001$) than males ($\overline{X}$ = 24 October, SE = 1.5 days, $n = 39$). Means include data from subadults ($n = 5$ estimates for females, $n = 6$ estimates for males). A slight interaction between factors year and sex was detected when comparing dates of den entry ($F_{3,71} = 2.31$, $P = 0.08$).

Duration of denning of males ($\overline{X}$ = 184.6 days, SE = 3.8, $n = 26$) was significantly less (t-test, $t_{61} = 3.3$, $P < 0.001$) than that of females ($\overline{X}$ = 198.6 days, SE = 2.3, $n = 37$). Means include data from subadults ($n = 4$ estimates for females, $n = 3$ estimates for males).

5.3.3 Den Characteristics

I investigated 56 dens of barren-ground grizzly bears. All dens were excavated by bears in this study. No snow dens, surface dens, or natural cavities

were constructed or used by study animals. Further, no dens were thought to be re-visited or re-used by bears (i.e., all excavations were new). Most dens were composed of a single entrance, which widened after a short distance (<50 cm) into a large, circular den cavity or chamber. Two of 56 dens possessed noticeably long tunnels (>1 m in length) prior to widening into den cavities. By mid-summer the majority of dens had partially or fully collapsed (44/56), precluding measurements of some dimensions for several dens (e.g., entrance height and cavity height). Den dimensions are summarized in Table 5.1. Choice of den aspect was non-random ($\chi^2 = 12.4$, df 3, $P < 0.01$), with the majority of dens facing south (25/56), followed by west (13/56), east (10/56), and north (8/56). All dens were located on steep slopes ($\overline{X} = 25.3°$, SE = 1.2, $n = 55$).

More than any other plant species, dens were constructed under the cover of dwarf birch. Dwarf birch was present at 84% of den sites for which vegetation characteristics were recorded, and was highest in mean percentage coverage around den entrances (Table 5.2). The roots of dwarf birch were observed to form the ceilings of several den entrances and were sometimes visible in the ceilings of cavity chambers. Other common species near den entrances included typical tundra berry shrubs (crowberry, cranberry, and blueberry) and several species of grasses and sedges (Table 5.2).

Analysis of excavation piles of 54 dens revealed substantial use of sandy areas for denning (Table 5.3). Excavation piles contained lesser amounts of silt-clay and gravel than sand. Cobble and boulders in excavation piles were common, of which some boulders were very large (>50 cm diameter).

Table 5.1. Summary of dimensions (cm) recorded at dens of grizzly bears in the central Arctic, 1995–1999.

	Mean	SE	*n*
Entrance Width	60.4	2.1	27
Entrance Height	55.2	2.4	24
Cavity Width	140.3	6.3	26
Cavity Height	82.2	3.3	13
Den Length	261.4	13	29

Table 5.2. Proportional presence of plant species, mean proportional coverage of plant species, and SE of mean proportional coverage of plant species recorded for dens (n = 52) of grizzly bears in the central Arctic, 1995–1999.

	Proportion of Dens Containing Species	Mean Proportional Coverage of Species[1]	SE of Mean Proportional Coverage
Dwarf Birch (*Betula glandulosa*)	0.843	0.342	0.036
Willow (*Salix* spp.)	0.353	0.086	0.028
Crowberry (*Empetrum nigrum*)	0.725	0.161	0.025
Cranberry (*Vaccinium vitis-idaea*)	0.843	0.071	0.011
Blueberry (*Vaccinium uliginosum*)	0.588	0.041	0.008
Bearberry (*Arctostaphylos* spp.)	0.471	0.037	0.009
Labrador Tea (*Ledum decumbens*)	0.569	0.032	0.066
Alpine Azalea (*Loiseleuria procumbens*)	0.118	0.003	0.002
Saxifrage (*Saxifraga tricuspidata*)	0.059	0.003	0.002
Grass/Sedge	0.804	0.106	0.022
Moss	0.176	0.010	0.004
Lichen	0.059	0.004	0.003
Other[2]	0.608	0.104	0.028

[1]Standardized to exclude proportional cover of excavation pile and caved-in portions of den.
[2]Includes exposed soil and rare occurrences of identified and unidentified plant species.

Table 5.3. Mean proportions of soil components (as in Soil Classification Working Group 1998) and their standard errors recorded at excavation piles of dens (n = 54) of grizzly bears in the central Arctic, 1995–1999.

	Mean	SE
Boulder	0.039	0.011
Cobble	0.076	0.014
Gravel	0.065	0.025
Sand	0.588	0.054
Silt	0.242	0.048

Most dens (37/56) contained substantial amounts of nest or bedding material, which was observed to be gathered by bears immediately prior to entering dens. Bedding material was often, but not always, removed from den cavities onto excavation piles, presumably upon exit by the bear. This leads me to believe that bedding material may have been used to plug den entrances once bears entered dens, in addition to providing a sleeping nest for bears within dens. Bedding material was composed primarily of mats of crowberry, dwarf birch, and moss.

5.3.4 Denning Habitat

Bears entirely avoided denning in five of the 12 major habitat types available to them (wetlands, tussock/hummock successional tundra, lichen veneer, boulder fields, and exposed bedrock). Esker habitat, which previously had been regarded as a major denning habitat for barren-ground grizzly bears (Mueller 1995; Banci and Moore 1997), accounted for seven of 56 den sites. The remaining dens were located in typical heath tundra habitat (23/56), tall shrub riparian habitat (3/56), birch seep (5/56), spruce forest (5/56), heath tundra habitat with >30% boulder content (11/56), and heath tundra habitat with >30% bedrock content (1/56). One further den was located in a non-vegetated sand embankment adjacent to the Hood River. Compared to the proportional availability of habitat types in the three Landsat TM images used in the habitat analysis (Table 5.4), the selection of denning habitat by bears was determined to be significantly different from random ($G = 127.7$, df 6, $P < 0.0001$). Comparison of Bonferroni confidence intervals indicated that esker habitat was selected more than expected from chance ($0.10 > P > 0.05$). In addition to those

Table 5.4. Observed and expected number of dens in each habitat type for grizzly bears in the central Arctic, 1995–1999.

Habitat of den	Proportion of habitat in study area (p_i)	Observed no. dens in habitat ($n = 55$)	Expected no. dens in habitat ($p_i \times 55$)
Lichen veneer*	0.0243	0	1.34
Esker habitat	0.0077	7	0.42
Wetland *	0.0790	0	4.35
Tussock/hummock*	0.0946	0	5.20
Heath tundra	0.3200	23	17.60
Spruce forest	0.0025	5	0.14
Bedrock*	0.0352	0	1.94
Riparian tall shrub	0.0031	3	0.17
Birch seep	0.0108	5	0.59
Heath/boulder	0.1574	11	8.66
Heath/bedrock	0.1114	1	6.13
Boulder field*	0.1540	0	8.47

*Not included for statistical analysis as observed values of use are zero (see text).

habitats in which no dens were found, heath tundra with >30% bedrock content was avoided for denning ($P < 0.05$).

5.4 Discussion

Duration of denning probably has adaptive significance for grizzly bears; however, mechanisms that drive and control when and for how long grizzly bears den are unclear. Environmental factors are likely involved as evidenced by the lengthening of den periods along latitudinal and elevational gradients (e.g., Smith et al. 1994). For example, mid-October dates of den entrance and late-April dates of den emergence in the central Arctic compare similarly with barren-ground grizzly bears inhabiting the Arctic National Wildlife Refuge, Alaska (Garner et al. 1984), the Tuktoyaktuk Peninsula and Richards Island, Northwest Territories (Nagy et al. 1983), and the North Slope of Alaska (Reynolds 1980). But the duration of the denning season for these northern grizzly bear populations is considerably longer than for southern and Pacific-coastal grizzly bear populations. Grizzly bears inhabiting the East Front of the Rocky Mountains, Montana, enter dens in early November (median = 7 November, $n = 45$) and emerge from dens near the 7 April ($n = 43$) (Aune 1994), a full two and three weeks after and before den entrance and emergence (respectively) of bears in the central Arctic. Males and females on Chicagof and Admiralty Islands, Alaska, den on average one to two weeks later than bears in the central Arctic, although dates of den emergence are similar to this study (Schoen et al. 1987). The latest dates of den entrance are found for grizzly bears on Southwest

Kodiak Island, Alaska, where mean dates of den entrance for males and females are in mid-November and early December (Van Daele et al. 1990).

Environmental factors influencing the onset and duration of dormancy in bears may include specific weather conditions such as snowfall (Craighead and Craighead 1972), temperature (Rogers 1987), and scarcity of food. Milder winters, for example, may result in later dates of den entry or earlier than usual dates of den emergence, or even no dormancy at all (e.g., Kodiak Island, Alaska, Van Daele et al. 1990). In this study, the mean temperature for May in 1997 at Contwoyto Lake weather station in the central study area was 0.6•C warmer than in May 1996 (Environment Canada; http://www.cmc.ec.gc.ca). Both male and female grizzly bears emerged from dens significantly earlier in 1997 than 1996, possibly as a result of above average temperatures in spring 1997. Physiological factors linked to physical condition also may indicate readiness for denning or emergence. And age, which is related to body size, may influence duration of denning. For example, older and larger males likely den for shorter periods of time than subadults. In this study, however, subadult sample sizes were too small to measure an effect. Further, some endogenous control related to photoperiod may initiate a metabolic shift towards or from dormancy (Folk et al. 1976). Most likely, a combination of abiotic and biotic stimuli indicate when it is appropriate for grizzly bears to den, and when it is appropriate to emerge from dens.

Similar to most studies of grizzly bear denning habits, males in this study entered dens later and emerged earlier than females (see, e.g., Craighead and Craighead 1972; Schoen et al. 1987; LeFranc et al. 1987; Van Daele et al. 1990;

Craighead et al. 1995). Studies with larger sample sizes than those presented here were able to show clear differences between the dates of den emergence for females with and without cubs, especially when single females were compared to females with cubs-of-the-year (e.g., Schoen et al. 1987; Van Daele et al. 1990). For grizzly bears, males generally emerge first from dens, followed by single females and females that entered dens with young, followed by females with cubs-of-the-year (Craighead and Craighead 1972; Pearson 1975; LeFranc et al. 1987; Schoen et al. 1987; Craighead et al. 1995). Differences in duration of denning among males and females may result from differences in metabolic rates. Male bears, being larger and with lower metabolic rates than females, likely have less need than females to spend time in protective dens to maintain lean body mass during winter. Upon emergence, females with cubs-of-the-year may require more time to lead young away from the safety of the den than do females with yearling or older cubs. There is also likely some advantage for females with cubs-of-the-year to suckle their young and allow them to grow within the den for as long as possible before vacating the den. Adult grizzly bears do not appear to require food immediately after leaving dens, and may be anorectic for up to three weeks post-emergence (Nelson et al. 1983). I suspect that a female with cubs-of-the-year will remain in or close to her den until she is forced to leave the den in search of food herself, which may not be necessary until weeks after bears of different reproductive status have left their dens.

In addition to timing and duration of denning, choice of den site is expected to have adaptive significance for grizzly bears. Grizzly bears use stored fat to survive during winter, and the ability to minimize loss of body fat during dormancy in part

determines a bear's ability to survive during winter (Folk et al. 1972). Apart from decreasing metabolic rate, grizzly bears can minimize energy loss to the environment during dormancy by choosing the most appropriate sites for denning. The best sites for denning may depend on several factors, including den aspect, slope, and habitat characteristics such as vegetation cover and soil substrate.

The generally southern aspect of den entrances observed in this study agree with the results of previous accounts of the aspect of grizzly bear dens in the central Arctic (e.g., Mueller 1995; Banci and Moore 1997). A southern aspect to den entrances may take advantage of northerly prevailing winds during winter, which can produce large snow banks on lee (southern) slopes. Large snowbanks covering den entrances likely help protect and insulate dens from the very cold temperatures experienced in the study area during winter.

The average slope into which dens of study animals were excavated was steep (>25%). Dens may be easier to dig on steep slopes, where soil may be exposed resulting in a deeper active layer (i.e., a deeper layer of thawed soil above permafrost) than in more level areas. In addition, den excavation on steep slopes may allow for dens to be constructed on near-horizontal or even upward-sloping planes, creating a warm-air trap in nest cavities (Harding 1976).

Steep, southerly-facing slopes also often produce well-developed patches of dwarf birch and berry-producing shrubs. In this study, dwarf birch and crowberry had the highest percent coverage of any plant species around den entrances. The roots of these shrubs may add to the structural integrity of den cavity ceilings. Mats of crowberry were also the main component of the insulating bedding material found

in the majority of grizzly bear dens. The high presence of grasses around dens in this study may be attributed to the colonizing abilities of these plants after disturbance. Most dens were not investigated until July, after, it appeared, that grasses had colonized excavation piles.

Grizzly bears in this study appeared to den in mainly sandy soil, sometimes with silt-clay and cobble content. Sandy soils may provide better insulation than very fine silty or clay soils. Gravel may be too loose for the construction of structurally sound dens.

Although dens were constructed in eskers only seven of 56 times, compared to the availability of eskers in the environment esker habitat was selected for denning more than what was predicted by chance. Typical heath tundra, heath tundra with >30% boulder content, spruce forest, tall shrub riparian areas, and birch seep areas were used in a manner consistent with what could have been expected from random habitat use. It should be noted that due to the small pooled sample size of dens ($n = 55$), power for Bonferroni confidence intervals in the habitat analysis was low ($1 - \beta < 0.80$). Due to their large contributions to the *G*-statistic, however, bears are likely preferring to den in spruce forest, tall shrub riparian, and birch seep habitats but the statistical power needed to demonstrate this is pattern lacking. Not surprisingly, no dens were observed in tussock/hummock meadows, wetlands, or boulder and bedrock fields, likely because of poor digging substrate and/or poorly drained soils. Heath tundra with >30% bedrock may have been avoided as denning habitat due to shallow digging substrate.

Previous studies (e.g., Mueller 1995; Banci and Moore 1997) suggested that large glacio-fluvial deposits such as eskers were extremely important for grizzly bear denning habitat. For example, Mueller (1995) reported that 29 of 32 bear dens encountered during surveys (91%) were located in eskers, when esker habitat was expected to make up 1.5% of the surrounding landscape. Banci and Moore (1997) reported finding 34 of 52 bear dens (65%) in eskers, mainly from unknown and uncollared bears. Such exclusive use of esker habitat for denning is not supported by data obtained from radio-collared grizzly bears in this study. Although bears are denning in eskers or other glacial-fluvial habitats such as kames and drumlins, and they are doing so to an extent greater than expected by chance, the use of eskers reported here is considerably less than what has previously been reported in the central Arctic.

One reason for the disparity between the results obtained in this study and those of Mueller (1995) and Banci and Moore (1997) may be lie in differences in methods of data collection. Both Mueller (1995) and Banci and Moore (1997) relied heavily on ground and aerial searches of older (>1 year) den sites of uncollared, unknown grizzly bears. Based on differences in the visibility of den sites among different habitats, however, the probability of identifying den sites from aerial and ground searches likely differs among habitats searched. Dens in eskers, for example, are easier to identify from the ground or air than dens in heavily-vegetated habitats such as tall shrub riparian areas. Bias in ability to correctly identify den sites equally among all habitats available to bears questions the validity of results of den surveys based on searching for dens of unknown bears. Further, habitat types were not

equally searched, according to availability, during den surveys in both Mueller (1995) and Banci and Moore (1997). Mueller (1995), for example, spent 53% of the time searching the relatively rare esker habitat for dens. Not surprisingly, Mueller's (1995) data was biased towards finding dens in eskers. By using radio-telemetry to collect data on denning habits of grizzly bears, I eliminated biases associated with the aerial and ground surveys of Mueller's (1995) and Banci and Moore's (1997) studies.

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6. GENERAL DISCUSSION AND MANAGEMENT IMPLICATIONS

6.1 Spatial Organization of Barren-Ground Grizzly Bears in the Central Arctic

In this thesis I examined two aspects of the spatial organization of barren-ground grizzly bears (*Ursus arctos*) in Canada's central Arctic. First, in Chapter 2, I tested the geographic bounds of possible sub-populations of grizzly bears in the study area (Chapter 1; Fig. 1.1). Then, in Chapter 4, I described patterns of home range size for grizzly bears.

The results of Chapter 2 suggest that grizzly bears in the study area, particularly males, are capable of traversing great distances (Chapter 2; Figs. 2.2 and 2.3). I documented high rates of immigration and emigration among identified population clusters (Chapter 2; Fig. 2.8). These observations led me to conclude that barren-ground grizzly bears in the central Arctic cannot be divided into geographically distinct demographic units (i.e., sub-populations). From data presented in Chapter 2, I anticipated that barren-ground grizzly bears in the central Arctic would possess large, continuously overlapping home ranges.

Analyses presented in Chapter 4 confirmed that home ranges of bears in the study area are relatively large compared to other grizzly bear populations. In fact, the home ranges of barren-ground grizzly bears in the central Arctic are the largest ranges

yet reported for grizzly bears in North America. Further, overlap among home ranges of female bears in the central Arctic is indeed high relative to females of more interior grizzly bear populations (McLoughlin et al. 2000). Large home ranges and high home range overlap describe the spatial organization of barren-ground grizzly bears in the central Arctic.

The spatial organization of grizzly bears is likely affected by habitat quality, where habitat quality may be defined by the general abundance and predictability of food in time and space. For example, the population level review I presented in Chapter 4 demonstrated a significant inverse relationship between mean home range size of grizzly bears and primary productivity for study areas in North America (Chapter 4; Fig. 4.4). Further, like home range size, home range overlap appears to be linked to habitat quality. Among populations of grizzly bears in North America, populations in areas of low seasonality, such as Pacific-coastal regions, exhibit high home range overlap (McLoughlin et al. 2000). Areas of extreme seasonality, such as the central Arctic, also support populations of grizzly bears with high home range overlap (McLoughlin et al. 2000). However, in areas of moderate seasonality, as one may find in more interior North America, home range overlap of grizzly bears is relatively low (McLoughlin et al. 2000). Thus, among grizzly bear populations in North America, there appears to be a positive relationship between home range size and habitat quality but a non-linear relationship between home range overlap and habitat quality.

McLoughlin et al. (2000) presented and tested a conceptual model to explain this curious variation in spatial organization among populations of grizzly bears. It is

worth presenting this model here as it may explain the evolution of spatial organization in barren-ground grizzly bears of the central Arctic.

For food-maximizing (Schoener 1971) and solitary animals (e.g., adult female grizzly bears), the spatial organization of individuals in response to changing habitat quality may be depicted as in Fig. 6.1. Here, habitat quality may be defined by factors that include food abundance (e.g., primary productivity) and predictability of food in time (e.g., seasonality) and space (e.g., patchiness). Areas of high habitat quality contain abundant foods that are predictable in time and space. Areas of low habitat quality contain low and/or unpredictable food resources. Areas of moderate habitat quality show intermediate levels of food abundance and predictability.

The model makes the following predictions. First, in areas of high habitat quality (Fig. 6.1A) populations are characterized by small home ranges and high home range overlap. Small home ranges occur where food is abundant or predictable because animals will be able to maximize energy intake over less area, with or without territorial defence (Hixon 1980). Further, there may be no selective pressure to defend areas if limiting food resources are in regional superabundance and expelling intruders does not improve an animal's access to food (Gill and Wolf 1975; Carpenter and MacMillen 1976; Carpenter 1987). Under some circumstances, increases in competitor density and thus intruder pressure—an indirect result of increased food availability—may make effective territorial defence impossible (Myers et al. 1981). Fig. 6.1A summarizes the situation of grizzly bears inhabiting Pacific-coastal regions of North America, where home ranges are among the smallest

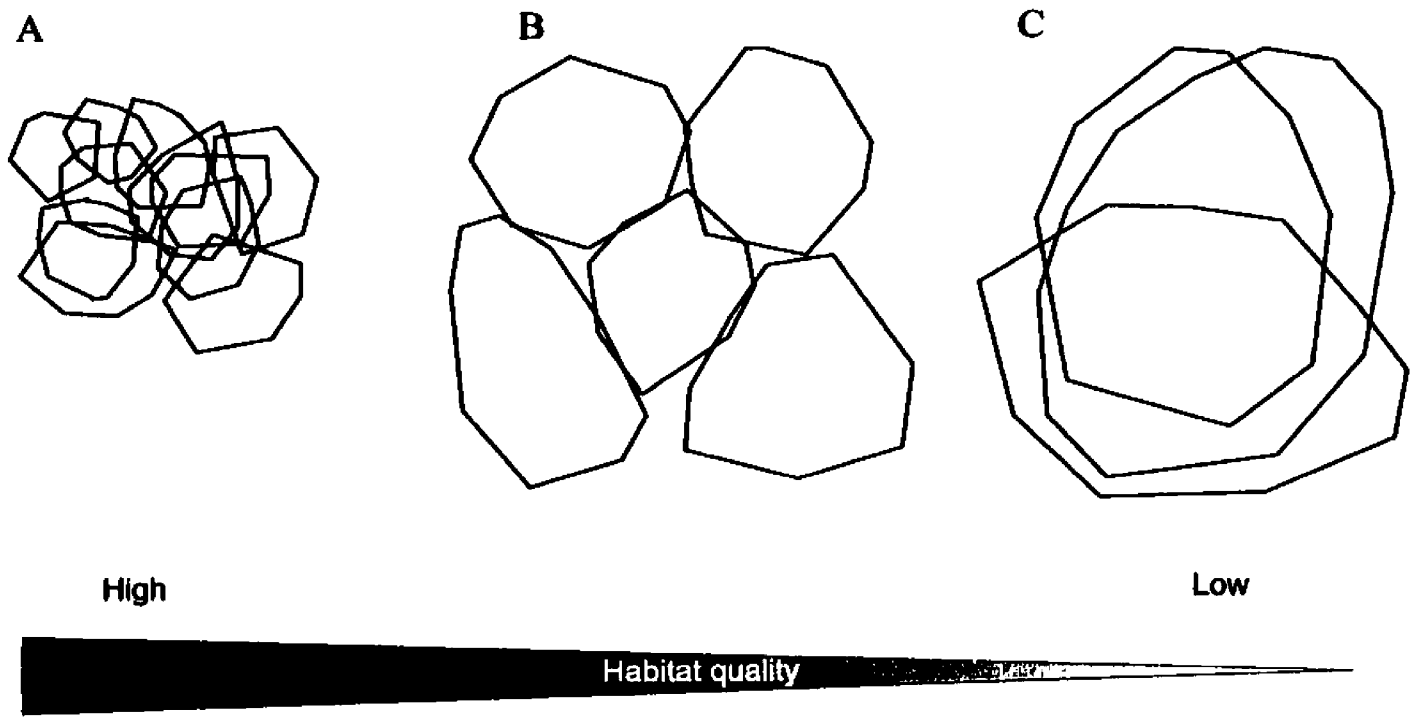

Fig. 6.1. The spatial organization of individuals varies along a continuum according to habitat quality, which can be defined by the abundance and predictability of food resources. A. In areas of high quality habitat, populations are characterized by high densities, small home ranges, and high home range overlap. B. In areas of intermediate quality habitat, populations are characterized by intermediate densities, moderately-sized home ranges, and low levels of home range overlap. C. In areas of low quality habitat, populations are characterized by low densities, large home ranges, and high home range overlap.

on the continent, density is highest, seasonality is low, and primary productivity is high (McLoughlin et al. 2000).

Second, the model predicts a shift to larger home ranges and a decrease in home range overlap as habitat quality decreases from high to more moderate levels (Fig. 6.1B). Larger ranges are needed to collect more variable or less abundant food. Spacing behaviour should be adopted when habitat quality drops to more moderate levels, as it may now be economically feasible for animals to defend limited food resources (Carpenter and MacMillen 1976). This situation applies to the majority of grizzly bears inhabiting interior North America (e.g., the Rocky Mountains), where home ranges, density, seasonality, and primary productivity are at relatively intermediate levels (McLoughlin et al. 2000).

Third, the model predicts that home ranges will continue to increase in size as habitat quality decreases from intermediate to low levels, but home range overlap will increase (Fig. 6.1C). In areas of lower habitat quality, animals will abandon defence of their home range as resources may be so scant or unpredictable that economically there is no benefit in defending a territory (Carpenter and MacMillen 1976). This would be the situation for grizzly bears in the central Arctic and for other barren-ground populations of grizzly bears, where home ranges are large, density is low, seasonality is extreme, and primary productivity is low (McLoughlin et al. 2000). The space-use model presented in Fig. 6.1 provides an example of how the environment may select for animal behaviour. Patterns of life history and behaviour may vary over time and space with environmental change. The ability to adapt life history and behavioural patterns to changes in the environment enables species to

occupy wide distribution ranges and heterogeneous environments. For solitary, food-maximizing animals—such as adult female grizzly bears—the model demonstrates how space-use may vary with changes in the environment. The model helps explain why we find large, overlapping home ranges for grizzly bears in the central Arctic and other barren-ground regions in North America, but sometimes different patterns of spatial organization for grizzly bears throughout the rest of the continent.

6.2 Habitat Selection Patterns of Barren-Ground Grizzly Bears in the Central Arctic

In Chapter 3, I examined the habitat selection patterns of grizzly bears in the central Arctic. I was careful to consider more than one scale of habitat selection, as study conclusions may depend on the spatial or temporal scale of observation (Allen and Starr 1982; O'Neill et al. 1986; Wiens 1989; Duarte 1991; Levin 1992; Allen and Hoeskstra 1993). For example, factors affecting survival and reproduction can differ from one level of habitat selection to the next (e.g., Orians and Wittenberger 1991; Schaefer and Messier 1995; Rettie and Messier 2000). Rettie and Messier (2000) suggested that selection patterns for animals should permit them to avoid the effects of those factors most able to limit individual fitness, and selection patterns that allow for this should be strongest at the coarsest (largest) scales. Therefore, the selection of habitats at larger scales may differ from the selection of habitats at smaller scales. Failure to view habitat selection as a hierarchical process could result in a narrow and possibly misleading notion of the value of habitats to animals.

I documented highly selective patterns of habitat selection by barren-ground grizzly bears. Using resource selection functions (Manly et al. 1993; Boyce and McDonald 1999), habitat selection was demonstrated at both Johnson's (1980) second and third orders of selection (i.e., among home ranges and within home ranges, respectively). The general pattern was for bears to preferentially select esker habitat, tall shrub riparian habitat, tussock/hummock successional tundra, and lichen veneers relative to other habitat types for both orders of selection. Although habitats selected at the second order (coarser scale) were largely selected at the third order (finer scale) of selection, scale differences in habitat selection patterns were documented in this study. For example, some habitats, such as tall shrub riparian habitat, which was only moderately preferred at the coarser order of selection, became highly preferred at the finer order of selection. Also, no differences in the habitat selection patterns between males, lone females, and females with accompanying young were found to occur at the second order of selection, but differences in habitat selection between sexes were found to occur at the third order of selection. These results underscore the importance of acknowledging scale dependence in habitat selection.

Understanding the hierarchical nature of habitat selection and the relative importance of habitats to animals, while in itself of interest to ecologists and wildlife managers, may actually be only the first step in detailing further aspects of the ecology of organisms. Recently, Boyce and McDonald (1999) highlighted procedures that can be used to relate resource selection functions to mapping the abundance of organisms using geographical information systems (GIS) and for estimating total population size in an area. The general approach is to extrapolate

population size for a study area with known areas of resource units through the use of resource selection functions calculated for a smaller reference area with known populations size. This procedure may prove useful for the mapping of grizzly bear abundances in the central Arctic based on resource selection functions.

Before we can estimate the abundance of bears in the study area using resource selection functions, however, we must concern ourselves again with the hierarchical nature of habitat selection. At what level of selection should resource selection functions be used to estimate abundance of animals? How would estimates of population size change when resource selection is viewed from different spatial and temporal scales? More than one representation of population size could be obtained using different sets of resource selection functions, calculated at different levels of selection. Because different processes may drive selection patterns at different scales (Orians and Wittenberger 1991; Schaefer and Messier 1995; Rettie and Messier 2000), abundance estimates derived from higher order selection analyses may differ from abundance estimates derived from analyses based on lower orders of selection.

For example, consider that barren-ground grizzly bears in the central Arctic are probably food-limited. There is probably no other limiting factor of greater importance to the population. Habitat selection at the highest order of selection should ensure the provision of foraging habitat in the home range. Habitats selected at the higher order of selection may be magnified at lower orders of selection; hence the finding that resources selected at the second order of selection were also selected at the third order of selection (Chapter 3). However, at lower orders of selection, less

important limiting factors to the population may affect habitat selection patterns. Here, at finer orders of selection sexual segregation among habitats was evident, possibly a strategy to avoid intraspecific predation (Chapter 3). Scale differences in selection patterns exist for barren-ground grizzly bears, and extrapolations of population size from resource selection functions following Boyce and McDonald (1999) may differ according to the scale of resource selection functions used.

To take another example, in a recent study, Walton et al. (2000) established that eskers were highly selected by tundra wolves (*Canis lupus*) in the central Arctic at the second order of selection. Walton et al. (2000) concluded that eskers were important for wolves when they established home ranges, possibly because esker denning habitat may be one of the more important limiting factors for wolves in the central Arctic. Recall that selection patterns for animals should permit them to avoid the effects of those factors most able to limit individual fitness, and selection patterns that allow for this should be strongest at the coarsest (largest) scales (Rettie and Messier 2000). Habitat selection analysis within the home range (i.e., at the level of third order selection), however, showed that eskers were not used by wolves more than expected. In fact, selection for habitat was not overly strong at the third order of selection, possibly because when it comes to selecting daily or hourly patches of habitat in which to forage, wolves, as strict carnivores of mobile prey (such as migratory caribou, *Rangifer tarandus*), may not be tied to specific habitat types. Now, let's suppose we attempted a population size extrapolation as outlined by Boyce and McDonald (1999). On the one hand, by using higher order selection functions to extrapolate population size, we might expect wolf population size to be a function of

esker availability. Areas with higher esker availability would suggest higher wolf density. On the other hand, by using finer order selection functions to extrapolate population size, areas with high coverage of eskers would not necessarily predict high numbers of wolves.

For the above two cases, which method of estimating population size (i.e., one based on higher order and one based on lower order resource selection functions) would more closely approximate the true number of wolves in a study area? I would surmise that the estimate based on higher order selection functions would better estimate true population size, possibly because population size may respond to the processes that produce higher order selection patterns (e.g., food availability, need for denning habitat) more strongly than processes that yield selection patterns at finer scales (e.g., intraspecific predation, decisions of where to hunt mobile prey).

For some populations, it may not matter what order of selection resource selection functions are used for estimating population size. The influence of a limiting factor may persist over a broad range of scales (i.e., a broad domain) if its effects are not overcome by another limiting factor at the coarsest scale at which it is encountered (Rettie and Messier 2000). In such situations, selection patterns at smaller scales may continue to reflect selection patterns at coarser scales, and estimates of population size based on resource selection functions from different scales may not differ by any great extent. For example, consider the habitat selection functions derived for woodland caribou in Rettie and Messier (2000). Higher order selection functions detailed in Rettie and Messier (2000) implied that caribou selected for areas with lower numbers of wolves; wolf predation was likely the most important

limiting factor to their population under study. Lower order selection functions for caribou also largely reflected patterns consistent with predator avoidance. Here, I would predict that if one were to estimate population size through extrapolation of resource selection functions as in Boyce and McDonald (1999), estimates of caribou population size based on resource selection functions from second order selection analyses may not differ substantially from estimates of caribou population size based on third order of selection analyses. Here, as selection was similar across scales, I would recommend using those resource selection functions that showed the strongest selection for habitats to estimate population size.

6.3 Management Implications of Research

6.3.1 Population Delineation of Barren-Ground Grizzly Bears in the Central Arctic

If geographic bounds for a population can be clearly established, population size, demographic rates, and life-history parameters may be estimated with greater reliability from accurate estimates of immigration and emigration rates. Further, a greater number of methods are available to enumerate a closed (where births, deaths, immigration, and emigration are assumed to be zero), rather than open (no assumptions of demographic rates), population (Krebs 1989). If geographic bounds for a population cannot be established, then estimates of demographic rates must be obtained with discretion, and techniques of abundance estimation must be restricted. For example, the Cormack-Jolly-Seber technique (see Krebs 1989) is the only mark-

recapture method available to enumerate open populations; several other mark-recapture enumeration techniques are available if rates of immigration and emigration can be assumed to be zero (e.g., Lincoln-Peterson, Schnabel methods, Otis et al. 1978; Krebs 1989).

Poor population closure found in this study (Chapter 2) leads me to conclude that the grizzly bear population in the central Arctic should be treated as an open (continuous) population. The study area may still be divided and managed along the population boundaries identified in Chapter 2 for logistical and political reasons; however, it must be realized that management practices implemented in one management unit will likely affect adjacent units. In addition, the bear population in the study area is likely continuous with bear populations located adjacent to and outside the study area. Techniques of estimating population abundance for grizzly bears in the central Arctic should be restricted to those that do not assume population closure (e.g., Cormack-Jolly-Seber method, Krebs 1989; through the use of resource selection functions, Boyce and McDonald 1999).

6.3.2 Hierarchical Habitat Selection by Barren-Ground Grizzly Bears in the Central Arctic

Highly selected habitats, especially esker and tall shrub riparian habitats, should be regarded as important grizzly bear habitats. As such, these habitats should be considered by Government and industry when planning roads and infrastructures in the central Arctic.

Plans to map the abundance of barren-ground grizzly bears in the central Arctic using the methods highlighted by Boyce and McDonald (1999) are currently being considered. Drawing upon resource selection functions, it may be possible to estimate abundance of bears in the study area without a large-scale mark-recapture operation. One has to be careful, however, to take into consideration the level of habitat selection that resource selection functions were calculated when calculating population size. Following the methods highlighted by Boyce and McDonald (1999), more than one abundance estimate is possible for a given population by using resource selection functions from different scales of habitat selection. I would surmise that the estimate based on higher order selection functions would better estimate true population size, possibly because population size may respond to the processes that produce higher order selection patterns (e.g., food availability) more strongly than processes that yield selection patterns at finer scales (e.g., intraspecific predation).

6.3.3 Effect of Temporal and Spatial Differences in Habitat on Home Ranges of Barren-Ground Grizzly Bears in the Central Arctic

The relatively large spatial requirements of grizzly bears in the central Arctic agrees with results of other studies of barren-ground grizzly bears (e.g., Reynolds 1980; Nagy et al. 1983; Clarkson and Liepins 1989; Ballard et al. 1993), although ranges in this study are much larger than any previously reported range estimates for grizzly bears. Large ranges may put individual bears in contact with humans even when sites of human activity (e.g., exploration and hunting camps, industrial

developments, and communities) are of considerable distance from the core of the home range of an animal. Furthermore, individual ranges of barren-ground grizzly bears could encompass several camps that are tens or even hundreds of kilometres apart. Barren-ground grizzly bears, especially those of the central Arctic, may therefore be highly susceptible to human activity. Management of bears in the central Arctic should focus on maintaining low levels of human-caused mortality, with the realization that communities, hunting camps, and mining/exploration camps may impact bears from more than just the general vicinity. Estimates of bear population status and trends should be monitored in the region to ensure that the cumulative effects of human activity on bears, including mortality, are within sustainable limits.

6.3.4 Denning Ecology of Barren-Ground Grizzly Bears in the Central Arctic

In Chapter 5, I re-evaluated the importance of eskers and other habitats as denning habitat for grizzly bears in the central Arctic. I documented the denning habits of grizzly bears in the central Arctic by following satellite and VHF radio-collared bears to their dens. By using telemetry to collect data on denning habits, I eliminated some of the biases associated with aerial and ground surveys of dens of unknown bears. Previous studies using aerial and ground surveys of dens (e.g., Mueller 1995; Banci and Moore 1997) suggested that large glacio-fluvial deposits such as eskers were extremely important for grizzly bear denning habitat. Exclusive use of esker habitat for denning reported in these studies, however, is not supported by data obtained from radio-collared grizzly bears (Chapter 5). Although bears are denning in eskers or other glacial-fluvial habitats such as kames and drumlins, and

they are doing so to an extent greater than expected by chance, the use of eskers reported here is considerably less than what has previously been reported in the central Arctic.

That barren-ground grizzly bears are not as reliant on eskers for denning to the extent previously thought does not, however, warrant unmitigated use of eskers for the construction of all-weather roads and infrastructures in the central Arctic. It remains that grizzly bears do den in glacio-fluvial habitat, and do so preferentially *versus* other habitats. Further, Chapter 3 established that eskers are used extensively by grizzly bears throughout the year, not just for denning.

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